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RAPID MODIFICATION OF THE BEHAVIOR OF FISHES BY CONTACT WITH MODIFIED WATER

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I. INTRODUCTION

At the present time animal behavior is being studied from three or four more or less independent points of view: (1) the point of view of tropisms and reflexes or the study of specificities of behavior, (2) the point of view of positiveness or negativeness to environmental factors—an aspect of ecology or the interpretation of the relation of animals in their normal environments, (3) the point of view of speed or vigor of reactions and of reflexes in relation to the so-called physiological states and their modification—an aspect of physiology, because such states are due to physiological changes such as a change in the rate of metabolism, and (4), the point of view of the modification of behavior by repetition of action or repeated stimulations—an aspect of psychology. Such a separation of view points can be only provisionally made as all are probably resolvable into physiology. Most workers combine two or more of these points of view, so that one type or aspect of behavior acts as an index of another.

The first two view points noted deserve some comment. Specificities of behavior may be defined as those peculiarities of action which characterize species, genera, or even larger groups.

The senior author, for example, is able to distinguish some species of tiger beetles (about one-half inch long) occurring near Chicago, by their peculiarities of flight. Again, ornithologists depend much upon characteristic movements to distinguish species of birds. The details of action in the more stereotyped reflexes of Protozoa and other of the lower invertebrates, such as the backing and turning of Paramecium, are characters of species or of groups of species. These specificities have been much studied by some zoologists, but, like other specific characters, serve chiefly as material for the study of modification, and as characters to be used in cross breeding.

The point of view of ecology is the one of most recent development. It considers all phases of physiology that are related to the life of the animals in their natural environments. The behavior aspects which have been developed center around the following questions: (1) Do animals select their habitats? (2) Is the behavior of the same species different under different conditions? (3) Is there community of behavior among animals of the same or similar habitats? (4) To what factors of the environment do animals respond and what is the degree of the response to the different factors?

A relatively small number of investigations have answered the first three questions in the affirmative, for the particular cases studied. Studies on the effect of particular factors of the environment have been made, but usually with very small animals and under conditions which made accurate measurement and control of the experimental factors difficult. One of the most neglected aspects of physiology and behavior is the reaction of larger animals to the different factors involved in the surrounding medium.

From several points of view the importance of investigations at this point seemed sufficient to more than justify an attempt to determine whether or not fishes react to differences in the dissolved content of the water which they inhabit and whether or not different species differ in their reactions. The data relating to these two questions have been organized and published (Shelford and Allee, '13). Apparent rapid modification of the behavior of the fishes by repeated contact with the treated water was quite characteristic of their reactions and aroused interest sufficient to cause us to go over the results of one hundred experiments from the point of view of modification. This involved re-counting of movements and recalculation of time, etc., which, together with the examination of a large amount of literature has delayed the preparation of this aspect for several months.

II. CONDITIONS AND METHODS OF STUDY

The experiments were conducted under conditions as nearly uniform as possible with respect to all factors except the amount of the various solutes used. (For detailed plans and figure of the apparatus, see Shelford and Allee, '13, pp. 225–229). Two galvanized iron boxes, 120 cm. long by 14 cm. deep by 20.5 c.m wide, with screen partitions 5 cm. from the ends, making the in-

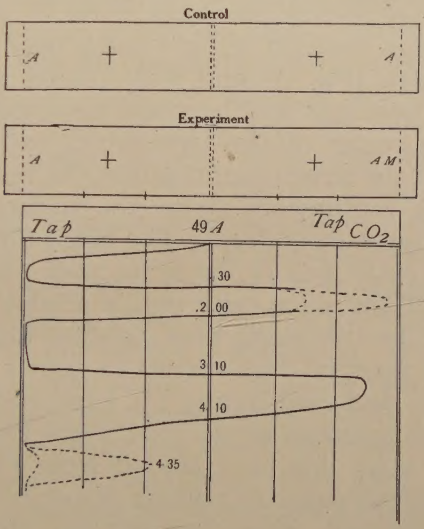

FIGURE I

The upper two quadrangles show the ground plan of the experimental tanks with the positions of the central drain and the lights under which the fishes went when passing to and fro. The positions of the lights are indicated by the crosses and that of the drain by the double broken line near the center. The broken lines near the ends indicate the positions of the screen partitions. The tanks are represented a little less than one-twentieth actual size. The ends *A* receive tap water and AM treated water. Below, the tank used for the experiment the method of recording movements is indicated. A portion of the record sheet is shown about twice natural size, and immediately below the reduced tank so that the marks dividing the tanks into sixths are opposite the corresponding dividing lines of the ruled paper. The movements of two mud-minnows during the first five minutes of expt. 49A are indicated with the time of the principal movements, in minutes and seconds after the beginning, shown in figures. The graph is an enlarged copy of the original . The solid line indicates that the two fishes were moving together; the broken line shows the movement of a single fish.

side length 110 cm., were painted dull gray and covered with yellow sand while still adhesive. Water was allowed to flow in at both ends at the same rate (usually 600 cc. per minute) through tees made from iron pipe, the cross bar of which contained a number of small holes. The cross bars of the tees rested on the bottoms of the tanks behind the screens. The drains were transverse tubes with their lower sides made of screen, located near the top and opening outside the boxes. The water flowed in at the ends and drifted toward the center at the top and flowed out through the drain. We found no evidence that fishes react to the slight current thus produced. Since each half of the tanks held about twelve liters, it required twenty minutes to fill them or to replace all the water in one of the halves.

Both tanks were enclosed under a black hood, side by side as shown in the plan (Fig. 1) and were placed about ten centimeters apart. Two four candle power incandescent lights were fixed above the center of the two halves, i.e., above a point midway between the screen partition and the center drain. The light was thirty centimeters above the surface of the water, which was ten centimeters deep. The lights above a given tank illuminated the outer wall of the other tank (see Fig. 1), while the inner wall of the same tank cast a shadow throughout its entire length. The two tanks were identical longitudinally, but the shadow was reversed with respect to points of the compass.

The room was darkened during the experiments, which were observed through openings in the hood above the lights. Fishes do not usually note objects separated from them by a light. The fishes not accustomed to aquaria sometimes showed fright and behaved erratically when first put into the tanks, but all such experiments were thrown out. The main stock of fishes was kept in the laboratory in glass-sided aquaria during the period of experimentation. In this way they became accustomed to an aquarium, to the presence of moving objects, and to variously placed lights.

The purpose of the experiments was to test the reactions of the fishes to a difference in the water in the ends of one of the experimental tanks. Water differing as little as possible from that in which the fishes usually live was introduced at both ends of the other tank in most experiments (control). Treated water from the device already described (Shelford and Allee, '13, p. 214), was introduced at one end of the experimental tank, while water differing as little as possible from that in which the fishes normally live was introduced into the other end. Various kinds of treated water were used as follows: (1) boiled water—oxygen, nitrogen, carbon dioxide, and bicarbonates in part removed; (2) water with varying amounts of carbon dioxide added; (3) boiled water with oxygen added (either against tap or boiled water at the other end); (4) boiled water with either carbon dioxide, acetic acid, or ammonia added. Various combinations of these factors were also tried and nitrogen was added in a few experiments.

When the difference between the solutes at the two ends of the tank was not great, we found by chemical tests that the central portion of the tank was a gradient between the characteristic waters introduced at the two ends. Usually the end thirds were essentially like the inflowing water. When the difference in concentration was great the region of the gradient was proportionally longer and the ends with the inflowing concentrations were accordingly shorter. When the difference in concentration was very great the entire tank was gradient.

During the experiments the two authors worked together. Three fishes were placed in each of two dishes containing enough water to barely cover them and set above the tanks. When all was in readiness and at a time agreed upon the two lots of fishes were emptied into the centers of the tanks. Marks on the sides divided the tanks into sixths. The fishes nearly always swam back and forth apparently exploring the tanks. The movements of the fishes were recorded graphically as shown in figure 1. For this purpose sheets of ruled paper were used. Three vertical double rulings correspond to the center and two ends of the tanks. Two pairs of single rulings divided the space between two primary rulings into three equal parts and the entire distance from right to left into six parts. Distance from right to left was taken to represent the length of the tanks; vertical distance to represent time which was recorded in minutes and seconds at the center. The width of the tanks was ignored. The graphs on the following pages are copies of the originals with the time corrected to scale.

Before or after the experiment, the headings of the sheets were filled in with data regarding the kind, size, and number of fishes, their previous history, the conditions in the tanks, concentrations of the solutes and other significant data. Details of the reflexes of the fishes and notable peculiarities of behavior were recorded in full at the left of the graph. The fishes were observed continuously for from twenty to ninety minutes. In many cases they were caught at the end of such a period of observation in a small hand net and replaced in the small dishes. Observers then changed places and transferred the fishes from one tank to the other. Thus the control fishes of the first experiment were observed in the experimental tank and the experimental fishes were observed in the control tank for a time equal to the first test.

III. EXPERIMENTAL RESULTS

Most of the fishes studied reacted negatively to various concentrations of carbon dioxide; to little oxygen; to boiled water with the removed oxygen restored; and to boiled water with acetic acid or carbon dioxide added (see table 3, p. 20). The behavior of the fishes when giving a negative reaction usually possessed prominent features. They tried the modified water a number of times and then began to turn back in the lower and lower concentrations of the gradient, or to spend shorter and shorter time in the modified water with each visit.

Usually these modifications did not show a uniform gradual decrease in time spent in the modified water or an increasing tendency to turn in lower and lower concentrations of the gradient which extended throughout the experiment. The response was rhythmic rather than cumulative. This may be seen in the charts especially in Expt. 10, chart 1, p. 9, and in controls 78 and 83, chart 2, p. 11. A number of successive trials of the modified water resulted in either a lessening of the time spent in that water or in turnings in the gradient, or both. This led to spending more time in the untreated water. After some time in this water there was again a tendency to enter the treated water with the same results as before. That is, there was a rhythm of reaction, which, while not perfect, was present to a recognizable degree in the majority of cases.

The number of trials of the modified water at the beginning of the experiment was in most instances inversely proportional to the degree of stimulation as indicated by the special activities, except where the concentration was great enough to cause "staggering," or other abnormal reaction. The control fishes on the other hand, went back and forth quite symmetrically.

The results of the experiments on each species were tabulated for the purposes of this paper as shown for the river chub in table 1, and for the golden shiner in table 2.

TABLE 1

Showing the varying speeds of the modification of the behavior of the river chub (*Hybopsis kentuckiensis* Raf, habitat, small, clear streams) associated with different kinds of modified water. The ratings given in column 3 represent degree of avoidance of the kind of water given first in column 2. The ratings were obtained by averaging per cent of time in the two halves and turnings from the two halves. The rating is 100 when all turnings were from one-half and all the time was spent in the opposite half, and 0 when time and turnings were equally divided between halves. These figures are taken directly from table 20, p. 256 of the preceding paper (of which see pp. 254-57 for further details*). The control rating for the species is ±0 based upon eleven controls.

Number of experiments	Kind of water used, the avoided water standing first	Rating	Difference in amount of oxygen at each end of the gradient in cc. per liter	Difference in amount of carbon dioxide at each end of the gradient in cc. per liter	Total number of individuals	Number of individuals showing modification	Number of invasions of modified water before first turning in gradient	Time in seconds in modified water from beginning to first evidence of modification	Time in seconds in untreated water
2	CO_2 in boiled vs. boiled	97	0	21	6	6	1.0		
2	CO_2 in boiled vs. tap	94	7	47	6	6	1.8		
1	CO_2 (weak) in tap vs. tap	87	0	5–8	1	1	3.0	110	30
2	CO_2 (strong) in tap vs. tap		0	18	8	6	1.3	169	510
3	Boiled vs. tap	67	7	2	9	9	3.7	95	221
2	Boiled vs. boiled plus oxygen	34	10	0	6	6	4.3	182	91
2	Boiled plus oxygen vs. tap	33	0	2	6	6	3.0	137	85
2	Boiled plus nitrogen plus oxygen vs. boiled plus oxygen. Nitrogen gradient 4 cc.	26	0	0	6	0			
	Totals and averages				48	40 83%	18.1 2.6	693	737

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* Corrections on p. 255 lines 12 and 13 for "tap water or water nearest like that in which they had been kept" read, more modified water.

Chart I

Showing modification of fish behavior by contact with boiled water, and with boiled with acetic acid added and with boiled water with ammonia added.

Distance between the small vertical lines adjoining the scales at the top corresponds to the length of the tank. The scales represent time in minutes divided into ten-second periods. The horizontal distances in the graphs represent the portion of the length of the tanks traversed by the fishes, the obliqueness of the line as measured by vertical distance and the vertical portions of the graph lines represent respectively the time required to move the distance and the time spent in resting or moving crosswise. The numbers above the generic names at the top represent the number of fishes used. When all or two of the fishes moved together a solid line occurs. The movements of single individuals are shown by broken lines. Double pointed arrows above the tracings indicate the distance occupied by the gradients. When the concentration was high the entire tanks were gradient and the secondary gradient is represented by the lighter double pointed arrows. A corresponding portion of the controls is likewise indicated. The kind of water introduced at the end indicated by the words "tap" and "boiled" the former being the kind of water in which the stocks here discussed were kept. The oxygen content of the water is given in cc. per liter in the vertical wordings where the amount of added solute is indicated also in cc. per liter excepting acetic acid which is given in grams per liter. For statistical purposes (Shelford and Allee '13) the proportion of time in the two halves, the number of turnings in the gradient are used as data.

In experiment 10 the fishes are shown to have entered the boiled water three times during the first two minutes, spending about one-half of their time there. At the end of the two minutes, they began turning back occasionally. This continued until the end of ten minutes when turning became the rule with more or less rhythmic entrance into the treated water. The experiment lasted forty minutes but the remaining ten minutes showed nothing different. When emptied into the control tank the fishes came to rest in one end and remained there for the first twenty minutes, a common reaction when the water is like that from which they were taken. At the end of the twenty minutes the fishes began moving back and forth in a symmetrical manner. Experiment 13 shows the reactions of sun fishes which are representative of the reactions of the fishes studied, to boiled water. The graph of experiment 41 shows a reaction to acetic acid comparable to that given to carbon dioxide. The reaction to ammonia might well be that of a control.

Since three fishes were used it was not always possible to distinguish the different individuals in the experiments and in working over the graphs. In the case of the gregarious species, all three nearly always moved together. With non-gregarious fishes it was nearly always possible to distinguish the different individuals in any one group of invasions of the stimulating water. Individuality was lost only in the periods of rest between invasions. After the graphs were made, the tracing of each fish was followed with red, blue or green ink, the individuals being followed so far as possible, but where individuals were lost during a period of rest each tracing was continued without conscious reference to what the individuals had done previously. This was due to the fact that the tracings were made as a basis for calculating time spent in the two ends and before any discussion of modification was in mind. The individuals are then, where not clearly distinguished, treated in a chance fashion, and should show the same average result as the actual movement of the individuals. The comparisons of species and factors are valid because such errors as occur are present in all the experiments and we believe that any errors arising from failures to distinguish individuals are of minor significance.

CHART I

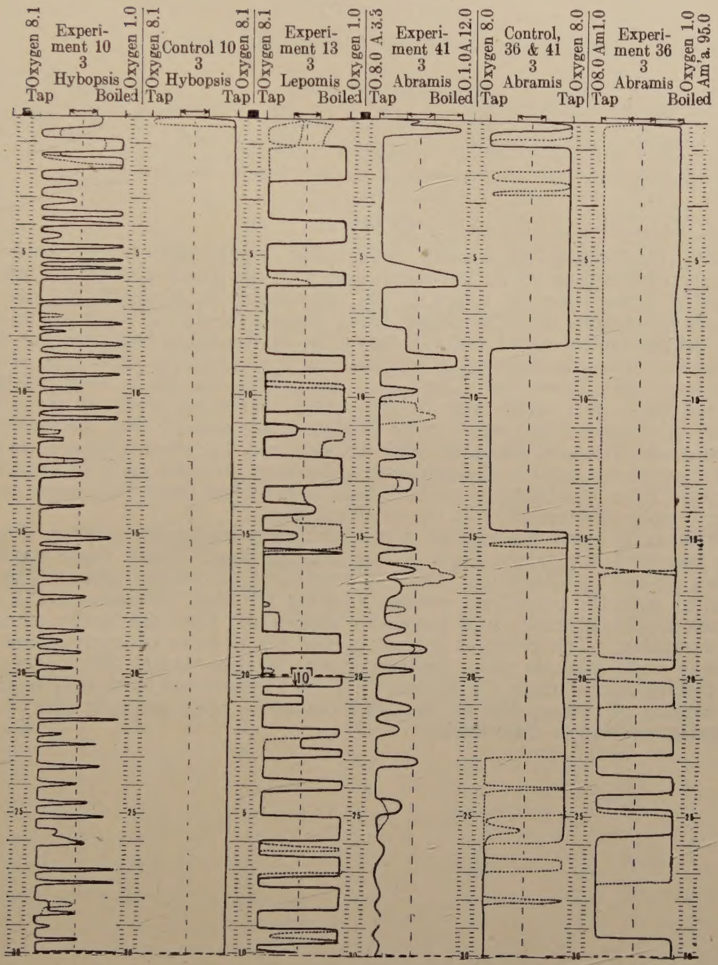
Oxygen 8.1 Tap
Experiment 10
3
Hybopsis
Oxygen 1.0 Boiled
Oxygen 8.1 Tap
Control 10
3
Hybopsis
Oxygen 8.1 Tap
Oxygen 8.1 Tap
Experiment 13
3
Lepomis
Oxygen 1.0 Boiled
O.8.0 A.3.5 Tap
Experiment 41
3
Abramis
O.1.0 A.12.0 Boiled
Oxygen 8.0 Tap
Control, 36 & 41
3
Abramis
Oxygen 8.0 Tap
O8.0 Am1.0 Tap
Experiment 36
3
Abramis
Oxygen 1.0 Am.'a. 95.0 Boiled
5
10
15
20
25
30
10

CHART II

Showing modification by contact with boiled water, with boiled water plus oxygen to balance that of the tap water, and with tap water plus carbon dioxide. For further explanation see Chart I. In experiment 78, *Hybopsis* did not react to the effect of boiling with the oxygen factor eliminated but did react to the boiled water. At the end of about two minutes after all the fishes had tried the boiled water several times, the turnings in the gradient began, and the same type of modification was again shown (see Chart I). *Ambloplites* reacted to both the boiled water and the boiled water with oxygen added. Detailed study of these fishes from the side in the boiled water while in glass boxes showed that the respiratory movement was increased but that other activity was depressed, this species being an exception in the matter of depression. However, in both parts of experiment 83, after the fishes had tried the water in both ends several times they began to turn back and make shorter stays in the modified water.

Experiment 53 shows the reaction where sufficiently high concentration of carbon dioxide was used to produce death in less than an hour. Under these conditions the fishes did not turn back until two had tried the high concentration. The third fish turned with the other two without entering the high concentration, a thing which takes place normally in a gregarious species and thus can hardly constitute a real exception. The graph is typical of the whole series of experiments until the end of eight minutes when the movements become erratic due to the effect of the carbon dioxide upon the fishes. In a later experiment with only a slightly larger amount of carbon dioxide the fishes ceased to react properly after a short time and turned upon their backs.

CHART II

Arrows indicate that the fishes were driven

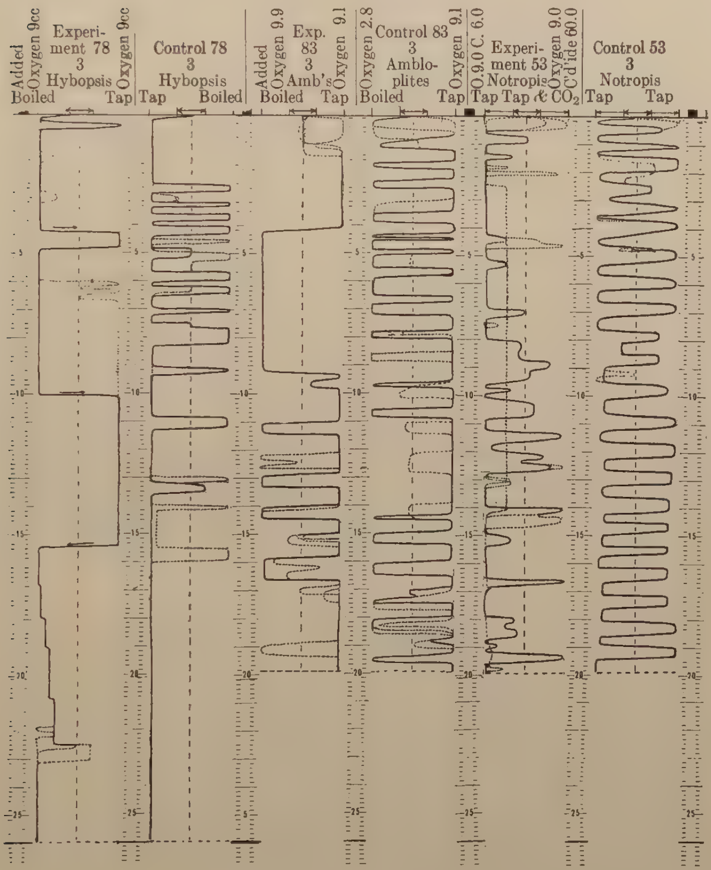

CHART III

Showing modification by contact with boiled water with 50 cc. per liter of carbon dioxide added. For further explanation see Chart I.

In these experiments the fishes tried the gradient of the entire tank a number of times and then either remained in one end except when driven as indicated by arrows, or turned back often before the center was reached. For example *Hybopsis* (experiment 56) entered the modified water once or twice and then came to rest in the low concentration, invading the high only when driven with the exception of a single excursion which followed a disturbance. The graph of *Ameiurus* shows one of the very few cases in which the fishes turned back before the strongest stimulus had been encountered. Still the graph brings out the same general fact of modification. The gradient in experiment 76 was established with some difficulty as the nitrogen was only 93% of the gas available the rest being oxygen. Boiled water had to be used at both ends and sufficient oxygen added at one end to balance the oxygen added with the nitrogen at the other. Even here, with the factors involved somewhat in doubt, the same modification is suggested.

CHART III

Arrows indicate that the fishes were driven

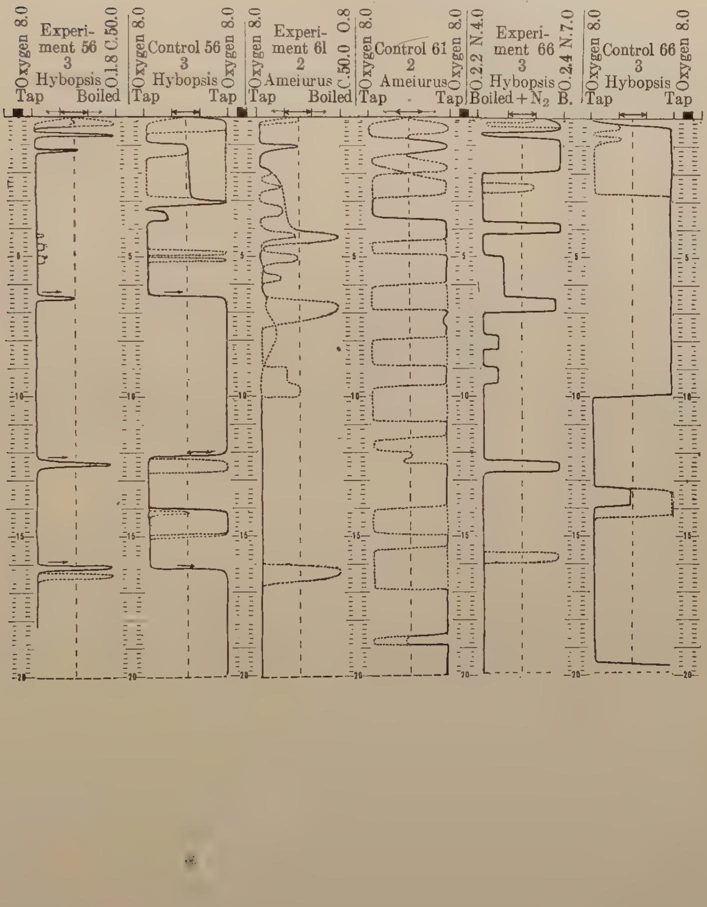

CHART IV

Showing the establishment of apparent preferences by groups of individuals of Abramis.

In experiment 1A an apparent preference already existed for the right hand end. An apparent preference for the left hand end was established and broken again by introducing boiled water as indicated. In experiment 84 the graphs of experiment and control are very similar during the first ten minutes. The apparent preference for the left hand end of the control tank was modified and apparently broken by repeated drivings indicated by arrows, and by confining the fishes in the avoided end during the nineteenth minute. The control fishes of experiment 58 established an apparent preference for one end after ten minutes and for reasons unknown. For further explanation see Chart I.

CHART IV

Arrows indicate that the fishes were driven

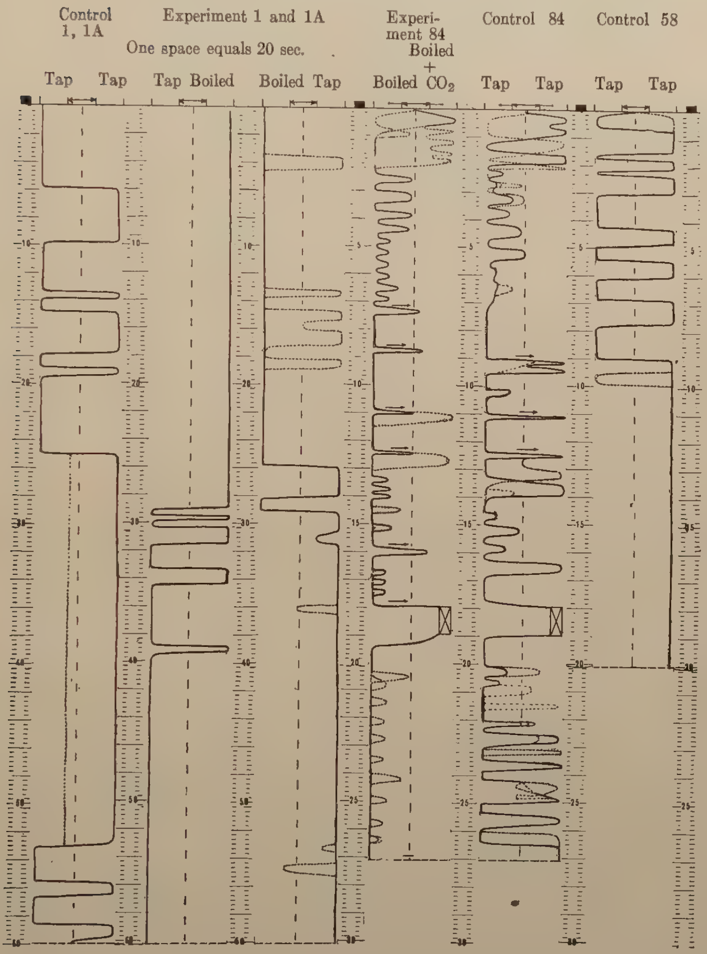

TABLE 2

Showing the varying speeds of modification of the behavior of the golden shiner (*Abramis crysoleucas* Mit. Habitat, stagnant ponds.). The rating of the controls ±11 is based on 15 controls. For further details see table 1.

Factor or factors, avoided water first	Rating	Difference in amount of oxygen at each end of gradient in cc. per liter	Difference in amount of carbon dioxide at each end of gradient in cc. per liter	Total number of individuals tested	Number of individuals showing modification	Number of invasions of modified water before first turning	Time in seconds in avoided water from beginning to first sign of modification	Time in seconds in untreated water from beginning to first evidence of modification
CO_2 in boiled vs. boiled. .	85	0	21	6	6	1.8	63	71
CO_2 in boiled vs. tap	91	7	47	6	6	3.6	52	268
CO_2 (weak) in tap vs. tap	60	0	5	3	3	2.0	43	62
CO_2 (strong) in tap vs. tap		0	65	6	6	3.5	66	96
Acetic 12 grms. per L. in boiled vs. 3.3 grms. per L. in tap.	85	7	2	2	2	3.0	215	485
Boiled vs. tap.	75	7	2	9	4	4.0	202	262
Boiled vs. boiled plus O_2. .	75	10	0	3	?			
Boiled plus O_2 vs. tap. . . .	39	0	2	3	?			
Boiled plus NH3 85 cc. per L. vs. tap 1 cc. per L.	8	7	2	2				
Totals and averages. . .				40	27 67%	17.9 2.98	641	1244

The behavior of Hybopsis is further illustrated in chart 1, Expt. 10, the data from which are included in the table. It will be noted that in the reaction recorded in the chart the three fishes first turned back after two invasions of the boiled water and that turnings occurred more often than entrances after fifteen trials of the boiled water. It will also be noted that the entrances of the boiled water toward the end of the experiment occurred only after some time had been spent in the untreated water. In this case there was less activity in the control as the fishes remained in one end for thirty minutes and then (see below graph of Expt. 13) began to go back and forth more slowly than in the experiment. Two turnings at the center are shown by the control fishes and these are opposite in direction. This shows that the fishes sometimes turn in the absence of solutes.

A comparable result with boiled tap water is recorded in chart 2, Expt. 78 (control). Here the turnings are less prominent and shortened stays in the boiled water were followed by resting in the tap water. In the part of Expt. 78, where the amount of oxygen was the same at each end of the gradient there is no evidence of modification, but simple disturbance is indicated. This shows that the fish sense the effects of boiling even when there is a normal amount of oxygen in the boiled water. In chart 3, Expt. 56, very rapid modification is indicated, and after the first few trials of the modified water the fishes stayed in the tap water end, except when driven out (indicated by arrows). In the same chart, Expt. 66 shows an apparent modification due to the introduction of an atmosphere of nitrogen and oxygen. This atmosphere had an oily odor which may have affected the results obtained.

Expt. 13 of chart 1 and Expt. 83 of chart 2 show the type of mild negative reaction with indications of slight modification given by the sunfishes and basses tried. The graph of Expt. 53, chart 2 shows the symmetrical type of control most common with Notropis and a case of somewhat erratic action in very strong carbon dioxide after it has time to seriously affect the fishes.

The graphs of Expts. 41 and 36 of chart 1 show the reaction of Abramis to acetic acid and ammonia in boiled water. On encountering the acetic acid the fishes often gave a definite reflex—the "backing-starting" reaction to be described on page 24. The reaction to acetic acid in boiled water compares very favorably with that to carbon dioxide in boiled water. Such a reaction is shown in Expt. 84, chart 4. The ammonia experiment shows the failure of the animals to react negatively to this factor, although the backing-starting reaction occurred more often than in the acid. The fishes died in the ammonia.

The case of Abramis demands special attention as this is the only species studied in which the groups of individuals developed apparent preference for unknown reasons. In this species this peculiar trait seems to be well developed. It avoids mild stimuli by rhythmically shorter stays in the modified water and stronger stimuli by turning back in the gradient. The general behavior when turnings are being given is shown in table 2.

In our earliest experiment with Abramis we obtained no results because the fishes remained in the tap water and so failed to encounter the treated water. It was noted also that when these fishes were left in the tanks they tended to stay in one end or the other. This led to the following experiment: Three individuals were placed in each tank with the same kind of water flowing into both ends of each. After both groups had developed an apparent preference for one end, the fishes selected for the control of the experiment to follow were disturbed until they tended to go back and forth. At the same time a shadow was thrown over the end of the tank selected for the experiment opposite to that in which the fishes were staying. The experimental fishes were driven into this shadow several times and soon developed an apparent preference for the shaded end of the tank. The fishes to be used for the experiment were left in the shadow for about two hours. The fishes to be used for the control were driven from end to end several times during this period. The apparatus was then arranged for the introduction of treated water which necessitated the removal of the shadow. Even after the shadow was removed and the apparatus was disturbed, the fishes persisted in their apparent preference for the end which had been shaded (Edinger, '01; Holmes, '11). Boiled water was introduced in the end in which the fishes were staying. The results of this part of the experiment are shown in Expt. 1-A, chart 4. In the control, the time was divided between the two halves in the ratio of 41 to 59 for the hour of the observation. During the same period the experimental fishes stayed in the boiled water end during the first 29 minutes, when they began going back and forth. They clearly stayed a little longer in the tap water with each excursion. After making five trials of the tap water in a trifle more than ten minutes the fishes came to rest in the tap water end and remained there until the completion of the hour's observation. The boiled water introducer was then placed in the newly "preferred" end and similar results were obtained modified only by the additional activity of a juvenile individual.

In Expt. 84, chart 4, the same species showed a comparable reaction. The control fishes avoided the end corresponding to the carbon dioxide end of the experiment as clearly as did those in the experimental tank. When they were confined in the avoided end the apparent preference for the other end was broken in the control, but only strengthened in the experiment. In the control of Expt. 58, Abramis established an apparent preference for the end avoided in Expt. 84. Since Abramis does not rest on the bottom, this reaction might be thought to be parallel to the resting of other fishes (chart 1, Expt. 10), were it not for the fact they that choose one end after visiting both many times, while others usually come to rest after the dash which follows their being poured into the tank. The behavior of Abramis in these controls was similar in many respects to the avoidance of carbon dioxide and acid given by this fish and others in the experiments. That is Abramis sometimes reacted positively to one end when tap water was running into the two ends from the same pipe at the same rate. The fishes do not appear to have any special tendency to rest near objects. They may sense the current at the end, but we have no evidence that such is the case.

These apparent preferences of Abramis demand further experimentation for their analysis. From the work so far they apparently do not belong in the same category as the rest of the reactions described here and may be due entirely to associative memory. Although if this be true the associated elements are at present unknown.

A general summary of the data on modification is contained in tables 3 and 4. In table 4, the various species are arranged roughly in the order of their sensitiveness. Later work by Mr. M. M. Wells has shown that the data in columns three and four are not accurate, because the time to loss of correlation or until "staggering" occurs is rather indefinite and difficult to determine. He uses the time until death. However, the data represent relative sensitiveness in a general way. The time required to accelerate the respiratory movements in low oxygen is likewise difficult to determine, but the data presented are more reliable than that in the two preceding columns. The remaining data are concerned with the number of trials before evidence of modification was given by turning. This is a definite criterion and does not seem open to serious criticism. Reading 6, 7, 8 and 9 from top to bottom, we note that generally speaking the less sensitive fish show the greatest number of trials of the modified water before giving evidence of modification. In columns 10 and 11, we note that the percentage of individuals showing modification is greatest in the more sensitive species and that when all are reduced to terms of 100 per cent. of modification the most sensitive species show the smallest number of trials before turning. The time in the two kinds of water is variable, but usually greatest in the unavoided water.

Reading the lines from left to right we note that the sensitiveness of the fishes is different for different stimuli.

TABLE 3

A list of the species used; the size of the individuals; physiological relations to the factors used; number of turnings and time spent in each half before modification was apparent.

1	2	3	4	5	6	7	8	9	10	11	12	13
SPECIES (Individuals used, chiefly juveniles)	Length of fish in centimeters	Seconds to loss of correlation in water with 1 cc. O_2 and 163 cc. CO_2	Minutes to loss of correlation in water with less than 1 cc. O_2	Seconds to modify respiration in water with 1 cc. of oxygen	Boiled CO_2 47 cc. vs. tap. No. trials before modification	Tap, CO_2 65 cc. vs. tap. No. trials before modification	Boiled vs. tap. No. trials before modification	Average number of trials before modification	Per cent showing modification	No. of entrances before modification reduced to basis of 100%.	Seconds in avoided water before modification. (Ave. of all expts.)	Seconds in avoided water before modification. (Ave. of all expts.)
Micropterus dolomieu Lac.	8– 9		20	40			6	6	100	6.0	257	215
Notropis cornutus Mit.	5– 9	60	376	45	1.0	0.8		1	100	1.0	97	108
Hybopsis kentuckiensis Raf.	7–10	50	355	50	1.8	1.8	3.7	2.3	100	2.3	251	108
Ambloplites rupestris Raf.	5– 9	180	340	55	1.0	1.5	5.4	2.6	58	4.5	200	119
Catostomus commersonii Lac.	8–11	300		60	1.3	2.3		1.8	60	3.0	95	110
Abramis crysoleucas Mit.	6–15		400	60	3.6	3.5	4.0	3.5	67	5.8	268	87
Etheostoma zonale Stor.	3– 5			150					0		20	20
Lepomis cyanellus Raf.	4– 6	150		300	2.3	3.5	2.5	2.8	60	4.6	146	165
Ameiurus melas Raf. Low O_2	13–15			350							5	
Ameiurus melas Raf. High O_2	13–15		1800	270		2.3		2.3	40	5.7	53	30
Umbra limi Kirt.	10–13						19.6				106	81
Totals					11.0	15.8	41.2	22.3	585	32.3		
Averages					1.8	2.2	6.8	2.8	65	4.0	159	104

In general the fishes were found by other criteria to be most sensitive to high carbon dioxide in boiled water, to high carbon dioxide in tap water, and to boiled water (low oxygen). It will be noted that the fishes showed modification with fewest trials of the type of water to which they are generally most sensitive. There are several exceptions to this, but the averages of all the species show this very clearly.

TABLE 4

Showing the speed of modification due to different conditions

	Experimental factors. Avoided conditions precede "vs"									
	CO_2 in boiled vs. boiled	Acetic acid in boiled vs. tap	CO_2 in boiled vs. tap	CO_2 in tap vs. tap		Boiled vs. tap		Boiled vs. boiled plus O_2	Boiled plus O_2 vs. tap	Boiled plus NH_3 (strong) vs. tap plus NH_3 (weak)
				Strong	Weak	High O_2 Stock	Low O_2 Stock			
No. of species tried..	2	1?	8	8	5	9	1?	6	6	2
No. of individual trials. Grand total, 230	12	4	38	45	9	35	23	33	27	4
Per cent of individual trials showing modification by turning	100	100	71	97	100	60	61	51	55	0
Ave. No. invasions of stimulating water before turning (modification)	1.4	2.7	1.8	2.1	2.1	4.4	3.8	4.7	5.5	
Ave. secs. spent in modified water before turning (modification)	30	147	30	119	62	205	86	99	174	
Ave. secs. spent in untreated water before turning (modification)	138	226	167	219	66	438	100	99	346	

Table 4 shows for the types of modified water shown in detail for all the species and individuals (230 in all). An examination of the table shows the same general relations as have been brought out for the particular species. The average time spent in the two kinds of water is least in the water producing the modification in all cases save one and in that the time in the untreated equaled that spent in the modified water.

IV. INTERPRETATION OF RESULTS

The phenomenon discussed and illustrated by the graphs on the preceding pages is clearly one of rapid modification. The behavior of the fishes was different after from one to four entrances into the end where the stimulation was greatest. This modification is indicated by the two types of behavior suggested above, viz.: (1) Turning in weaker and weaker parts of the gradient; (2) By making shorter and shorter stays in the modified water. This last type of behavior is not considered in the tables, since it cannot be readily tabulated because of its rhythmic nature.

In general, fishes swim about either continuously or periodically when in normal water and under uniform light conditions. This tendency under the unnatural conditions of the experimental tanks is strong and though some species may rest for considerable periods in the control tank, they periodically move from end to end. The fishes move crosswise of the tanks but this was not considered, since it appeared to be a minor matter because of the narrowness of the tanks. Furthermore, it bore no relation to the experimental conditions other than to prolong the time spent in a particular part of the tank.

The modification, which will be chiefly discussed, consisted of breaking the tendency to swim to the end of the tank and of substituting turnings at points of weaker and weaker concentrations of the experimental factor or factors. The tendency to pass to the end of the tank as opposed to turning nearer the center may not be markedly strong, for all the fish occasionally turned and swam back or swam about in circles without crossing the center (see chart 1, column 3, last ten minutes of the control of Expt. 10). Still, on account of the small size of the tanks, this tendency is apparently almost as strong as the tendency of fish to swim anywhere when not especially stimulated. No doubt it is about as strong as the tendency of Möbius' pike

(Holmes, '11) to strike its nose against the glass partition, and from the standpoint of the fishes in relation to nature, modification by contact with stimulating water is of a more significant type.

Any explanation of the modification demands first a clear statement of the problem. With figure 1 before us, this statement together with a discussion of various possible explanations will be made. One explanation that may be advanced is that the fishes were depressed by the modified water and thus tended to stop swimming forward on entering it and so finally came to rest in the normal water. This is very clearly not the case, although it is suggested by some of the graphs because the cross movements of the fish are not indicated. With one exception, the modified water was stimulating. The exception was a temporary depression of activity of the rock bass due to lack of oxygen. In a few experiments, the rock bass entered the boiled water and, being depressed, stayed there a half hour or more. Finally, however, they began to move back and forth and selected the tap water end.

Another explanation is that the fishes are stimulated by the modified water and thus move out of it more quickly and spend more time in the untreated water. This is clearly what happened in many cases. The fishes rushed forward more rapidly when they encountered the stimulating conditions, and upon reaching the end, turned and moved out quickly. Still, this does not explain the turning in the gradient which took place more often than the simple acceleration. Neither does it explain what was also sometimes true, namely, that fishes did not show the acceleration until they had encountered the treated water a number of times.

A third explanation that may be advanced is this: When the fishes had been exposed to the low oxygen water or to water containing much carbon dioxide for a long enough time to affect the oxygen or carbon dioxide content of much or all of the blood and thus affect the nervous system as a whole, the fishes began to turn back. The change in gas content caused a change in the physiological state of the fishes, so that they were more sensitive to the surrounding medium. In connection with this explanation, and the preceding one as well, certain facts brought out in the experiments should be noted. When dropped into water containing 150 cc. or more of carbon dioxide and only 1cc. of oxygen per liter, very striking evidences of stimulation appear almost instantly. In 47 cc. of carbon dioxide per liter in boiled water nearly all the fishes showed evidence of stimulation at once. They would start gulping before reaching the end of the tank on the first entrance of the solute. In only a few of the cases was this delayed as long as 50 seconds. In from 20 to 60 cc. of carbon dioxide per liter in tap water the fishes showed similar stimulation in from two to ten seconds after entering the high concentration. In boiled water some fishes showed increased activity, gulping within ten seconds, but such manifestations were frequently delayed for nearly a minute and were quite variable in intensity. In acetic acid the evidences of stimulation were similar to those in carbon dioxide and in ammonia some of them were noticeable.

The fishes undoubtedly sense the solutes upon entering them. For this, they give evidence by the following activities: A definite reflex was often given by Abramis, Notropis, Hypopsis and Lepomis the first time they entered the modified water. The fish suddenly stopped, backed quickly a few millimeters and then started ahead again, often repeating the reflex before going farther forward. In the earlier paper, we called this the backing-starting reaction. This may be due to stimulation of the nostrils. Sheldon ('09, p. 278) states that stimulation of the nostrils of the dog fish resulted in a quick jerk of the head. There was acceleration or increased vigor of movement of fins, tail or body which began at once or after a very short time. Sheldon found that the application of solutions to these parts caused them to be moved. The opercles were lifted, the lower jaw protruded, or the mouth moved in a manner characterized as coughing, gulping or yawning. Sheldon found that stimulation of the mouth or spiracle gave rise to violent gulps. In our experiments these reactions occurred singly or in combination. The time necessary to produce them was variable, but depended upon the strength of the stimulus, which confirms further observations by Sheldon ('09).

As further evidence of the quick sensing of the stimuli, Hybopsis turned back the first time the gradient was tried in nine cases, Notropis in three cases, Ameiurus in four cases, Umbra in one case, and Abramis in one case. With a single exception carbon dioxide was the factor thus avoided. This is good evidence that fish ascertain the condition of the water by peripheral sense organs or otherwise. The modifications appearing after a number of trials must be due to increased sensitiveness to the modified water or to associative memory or to both.

The physiological explanation which may be made for the increased sensitiveness with increased exposure to water high in carbon dioxide is simple, and is based largely upon the relations of organisms to carbon dioxide. The arterial blood of dogs and horses (Hill, '06) has been shown to contain 330–550 cc. per liter of carbon dioxide, free and combined. The free carbon dioxide is about 20 cc. per liter, so in most of the concentrations used more carbon dioxide would be taken up (Hill, '06, p. 533) and its removal from the blood and tissues was undoubtedly hindered in all cases. Since carbon dioxide is constantly produced inside the fish's body the effect of increased concentration on the outside would become greater with repeated trials of the carbon dioxide water. Waller ('96) has shown that carbon dioxide in small amounts increases the irritability of nerves. Hill ('09) states that similar results have been obtained with micro organisms.* A stimulating concentration of carbon dioxide is generally recognized among physiologists. Because of the increase in internal carbon dioxide brought about by entrance into the carbon dioxide water, the fishes tended to become more sensitive with repeated entrances and hence to turn back in weaker concentrations. After spending some time in the weaker carbon dioxide of the tap water end of the gradient tank, they partially recover and tend to resume their usual movements. This brings them again into the modified water and the process is repeated, hence we have a rhythmic invasion of the carbon dioxide water as shown in chart 1, Expt. 10.

As was noted in table 3, the respiratory center is stimulated and the respiration movements increased in carbon dioxide and in low oxygen. This requires more time than the reflexes which follow the sensory impressions (Westerlund, '06). In carbon dioxide the increased respiratory movements occur within a few seconds after the reflex movements. The same is true in low oxygen, where respiratory changes have been definitely timed (table 3). Our evidence indicates that peripheral stimulation is not of supreme importance in the regulation of breathing, because the fishes reacted definitely to a change in the water before the breathing was affected.

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*The sensitiveness of fishes to carbon dioxide probably increases with starvation. A stock of fishes kept during the winter of 1911–12 without food showed markedly low resistance in that they lost their equilibrium in from 30 to 50 cc. of carbon dioxide per liter.

Bethe ('03) proposed the hypothesis that the breathing rate of fishes is regulated directly by stimulation from the periphery, particularly by stimulation of the mucous membrane of the mouth and gills. This hypothesis has been widely tested (Baglioni, '10 and citations), but the more recent experimentation (Reuss, '10) seems to show that the breathing of fishes is regulated indirectly as in the higher vertebrates, although the suggestion of Kuiper ('07) that both the automatic center and reflex stimulation are concerned has much evidence in its favor. The important thing in the work of the followers of Bethe from the standpoint of this paper is the establishment of quickly working sense perception in the mucous membranes of the gills and mouth.

The negative reaction and modification of reaction of fishes to acid may be explained in a manner similar to that presented for carbon dioxide. Winterstein ('11), Signorelli ('10) and Quagliarello ('11) and others report that it is the acidity of the blood that affects the respiratory center and similar results are nearly always obtained with carbon dioxide and other acids in reversing reaction to light, etc. (Mast, '11 and citations). Accordingly the increased sensibility in acetic acid and in carbon dioxide probably have a common explanation.

It is well known that an insufficient supply of oxygen leads to the formation of lactic acid rather than carbon dioxide as the end product of respiration. Fletcher ('98), Fedman and Hill ('11) and Araki ('91) report that lactic acid production bears some inverse relation to oxygen supply. Signorelli ('10) found that lactic acid directly affects the respiration center.

When the fishes remain long enough in the low oxygen to affect the amount of oxygen in the blood and tissues, the presence of lactic acid probably results and the plasma tends toward acidity just as when acids are used directly. We thus infer that increased sensibility and the resulting modifications are due to acidity just as in the other two cases.

Ammonia is present in the blood of mammals and appears to bear some relation to the carbon dioxide (Hopkins and Dennis, '11). The failure of the fishes to react to ammonia accords with the known effects of the drug. According to Cushny, when ammonia or its common salts are absorbed by the blood, it is not rendered more alkaline but the ammonia is rapidly changed to urea and excreted. The effects of the kation on the common frog is to paralyze the terminations of the motor nerves. While the effect upon the sensory ending appears not to have been investigated, paralysis appears to have occurred in the fishes studied. Frogs and mammals usually die from ammonia poisoning in tetanic convulsions as did the fishes used in the experiments.

It may be noted that the stimuli which give rise to the modifications most quickly are those commonly encountered by fishes in nature. Ammonia, which is rarely encountered in any considerable quantity, did not give rise to a modification and not even to an avoiding reaction. Again the darters are swift stream fishes, depending upon mechanical conditions to maintain themselves in a suitable environment. They rarely encounter carbon dioxide or low oxygen and failed to react to them at all quickly, although they were affected by both. Advantageous reactions appear to be confined to stimuli commonly encountered in the normal life of the animal. By this we mean merely to imply that whatever the processes of origin and survival may have been in detail (Mathews, '13), there is correlation between the conditions of existence and types of irritability (Henderson, '13).

It thus seems probable that associative memory does not necessarily play any rôle in the process of modification described. Since the experiments were conducted with a view to eliminate any possible effects of learning, only incidental evidence was acquired. The treatment of the stock of fishes was as follows: There were a number of individuals of each species in the aquaria, and individuals were drawn at random for each experiment. A given series of experiments were run and the fishes were returned to the aquaria and not used for experiments until several days had elapsed. In nearly all cases the same fishes were used only by chance. When it was necessary to repeat an experiment on the same day, different fishes were used except in one or two cases not included here.

Apparently, in experiments thus conducted, evidence of retention can be of two kinds. These are indicated by the following questions: After entering the modified water a number of times and turning back, did the fishes often turn back before reaching the gradient ? When transferred to the control after exposure to the gradient did they turn back, or show a preference for either end of the control ?

The first type of behavior could be shown only where the gradient was confined to the central third of the tanks. Since some species turn in any part of the tanks it is necessary to select a particular species which does not show this trait. Hybopsis was our best example of this for normally they went back and forth symmetrically in the controls. The graphs indicate that in the boiled water experiments this species turned back often before the gradient was reached, which raises the question as to whether they associate the center drain or difference in lighting with stimulating water ahead.

Fishes are able to form associations (Möbius fide Holmes, '11 and many others). There appear to be two ways in which associations formed in the experimental tanks could be carried over to the control tanks. One is through the kinaesthetic sense, the other through differences in illumination of the sides of the body when approaching the drain from the different directions. The data which we have upon this question comes from comparing the responses in the first and second halves of the double experiments described on page 6.

It is obvious that if the fishes were able to associate the differences in illumination upon the sides of the body when approaching the drain, with increasing stimulation further on in the gradient and were able to retain this after being dipped out of the water with a net and placed for a short time in very different surroundings, they should show an apparent preference for the end of the control tank opposite that in which they spent most time in the experiment. (cf. Fig. 1). An examination of the records of twenty-eight controls indicates that the fishes usually showed some difference in their relations to the two ends of the control tanks, but in these exchanged controls less than half of the fishes show an apparent preference for the end that should have been favored if the light was depended upon. This is as it might be if the kinaesthetic sense were depended upon for the reaction, but the number of experiments is too small to make the slight difference more than a chance one. The comparison of the reactions in the experiment with those of the succeeding controls only serve to emphasize former findings that the solute is the chief guide in the reactions of the fishes.

Special investigation would be necessary to determine whether or not associative memory plays any rôle, but if so, it might be due to an association of increasing stimulation with stronger stimulation further on in the gradient. There is a more or less distinct rhythm of the reactions in the gradients and the view of associative memory applied to this phase of the reaction would call for a make and break of associations so rapid as to cast doubt upon this being the entire explanation. And, since the increased sensibility due to repeated stimulation is explainable otherwise, the assumption of learning, as applied to this aspect of behavior, is as unnecessary as it is questionable. Still, while we have thus separated the type of modification here described from associative memory by the use of the usual criteria, we do not mean to imply that the processes involved are necessarily fundamentally different.

IV. ACKNOWLEDGMENTS AND BIBLIOGRAPHY

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MODIFICATION OF THE BEHAVIOR OF LAND ANIMALS BY CONTACT WITH AIR OF HIGH EVAPORATING POWER

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I. INTRODUCTION

The rapid modification noted in the case of fishes, by the author and Dr. W. C. Allee is likewise shown by various land Amphibians and Arthropods, used in experiments designed to test the sensibility of different terrestrial animals to variations in evaporating power of air. Some animals of supposedly lower organization than the fishes, showed modifications similar in character.

II. MATERIAL AND METHOD

The following species were studied: the yellow margined milliped (*Fontaria corrugate* Wood), ground beetles (two species of *Pterostichus*), the wood frog (*Rana sylvatica* LeC.), the red backed salamander (*Plethodon cinereus Gr.*)—all from moist forest habitats; and the common toad (*Bufo lentiginosa*), the small digger wasp (*Microbembex monodonta* Say), the bronze tiger beetle (*Cicindela lecontei* Hald), and the sand spiders (*Geolycosa wrighti* Em and *pikei* Marx)—all from dry sand dunes.

The animals were put into small cages across which air was forced through three narrow slits. The ground plan of the cages is indicated in Fig. 1. The covers of the cages were of glass, the fronts opposite the slits of screen. Gradients of evaporating power were secured by passing air of different relative humidities, or different temperatures, or by passing it at different velocities across the different thirds. The device for thus controlling the rate of evaporation was designed by the writer and Prof. E. O. Deere of Bethany College. The statistical and environmental aspects of the one hundred experiments performed together with details of the methods were published elsewhere (Biol. Bull., June, 1913). Nearly seventy-five of the experiments were of such a character as to bring out the modification phenomenon. The tracings of the movements were drawn to a minute and second scale at the time of the observation (Fig. 1) and those presented here are original drafts. The different individuals could not be distinguished in a few cases, but since this error entered into all the experiments the results are constant for this piece of work. (For further discussion of this point, see Shelford and Allee, '14, p. 8).

III. EXPERIMENTAL RESULTS

To illustrate the method of obtaining and recording the data used further on, we present three charts. In Chart I, Expt. 71, the reaction of the red-backed salamander to increased evaporation in the right hand third of the experimental tank, is shown.

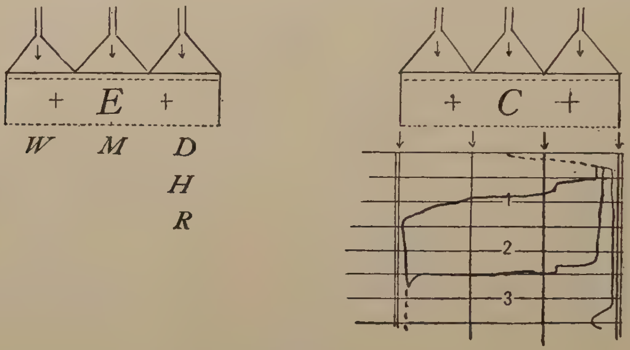


FIGURE I

Showing the ground plan of the experimental cages in their relative positions, the hood which covered and separated them is not indicated. E is the experimental cage; W, the section used for wet air; M, for the air supplied directly from the pump; D (dry), H (warm), and R (rapid flow), stand under the section where the highest rate of evaporation was maintained. The crosses indicate the positions of the 1 c.p. lights; the arrows the direction of the flow of air. The screen portions of the cage are represented by the broken lines. C, is the control cage, similar to the experimental in every way except the kind of air supplied. Below this is shown the control record of an experiment during the first three minutes. The ruling of the paper used corresponded to half minutes and the figures were written in at the center. The graph is about two-thirds natural size and the cages about one-seventh.

The increased evaporation is due to a rapid flow of ordinary air. The salamanders tried the region of highest evaporation repeatedly during the first fifteen minutes and then began to turn back when the rapid flow was encountered. We note that one individual turned back the first time it encountered the rapid flow. The control individuals came to rest practically where they were placed and moved only a little throughout the experiment.

The toads gave the same reaction to similar conditions. They tested the region of high evaporation repeatedly during the first ten minutes and then began to turn back and make short stays in that section. The control is a little less symmetrical than in most cases; for a more symmetrical control, see A, Chart IV, Expt. 42. Both species show a preference for low evaporation at the end of the period of experimentation. Chart II, Expt. 75, shows rapid modification of the behavior of the millipeds. (*Fontaria*). In the experiment, definite turnings began at the end of nine minutes, when each animal had entered the section of high evaporation. The control is a characteristic symmetrical graph for the species.

The graph of the spiders (*Geolycosa*) is difficult to interpret and is peculiar, due to the fact that the spiders are very quick and pugnacious, so that it is hardly possible for three of them to be in the same third of the cage at the same time. Still, even this graph appears to indicate what is true of single individuals namely, an avoidance of the moist and medium air. This avoidance does not begin until the end of eight minutes. The control is typical of the species and shows fairly symmetrical distribution of the spiders.

Chart III shows the reaction of the wood frog to gradients of evaporating power produced in three different ways. The graph of Experiments 60 and 70 shows the type which results from *acceleration* of *movement* or of *movement* due to mere *stimulation*. In Experiment 60, one of the frogs was placed in each third. Their commonest reaction to evaporation is to crouch close to the substratum. If, however, the evaporation continues, they finally hop, apparently at random. In the case of two of the frogs in Expt. 60, the hopping was in the direction of the lowest rate of evaporation where the frogs remained for an hour or more after the observations here graphed were ended. Experiment 70 shows first the stimulation of one frog leading to a series of hops in the direction of lower evaporating power, of another frog a little later in the direction of higher evaporating power which in turn led to stimulation, resulting in hops in the opposite direction. These graphs do not indicate modification. When compared with the next graph, where temperature was used to increase evaporating power, we note a striking difference (compare the graphs of Expts. 60 and 70 on the one hand and 73),

CHART I

Showing the modification of the behavior of the red backed salamander (Plethodon) and toad (Bufo) through a gradient of evaporation due to rapid movement of ordinary air in one section, the other two sections being supplied with respectively moist and ordinary air at the standard rate of flow (12 liters per minute, a velocity of .08 meters per second). The rapid flow was approximately .65 meters per second, or about 8 times the standard. The temperature is given in degrees centigrade. Immediately above the three columns of the ruled paper between the time scales is given the evaporation from the Livingston evaporimeters in hundredths of cc. during a period of 20 minutes immediately before and after the experiment. Distance from right to left represents the movements of the animals in the cage (lengthwise) and time is indicated by vertical distance as measured by the scales. The broken line is used where two or three animals move together. In the controls the large S's indicate that still air was used in the three sections.

CHART I

PLETHODON—AIR CURRENT 24°C
Experiment 71 Control

BUFO—AIR CURRENT—24°C
Experiment 68 Control

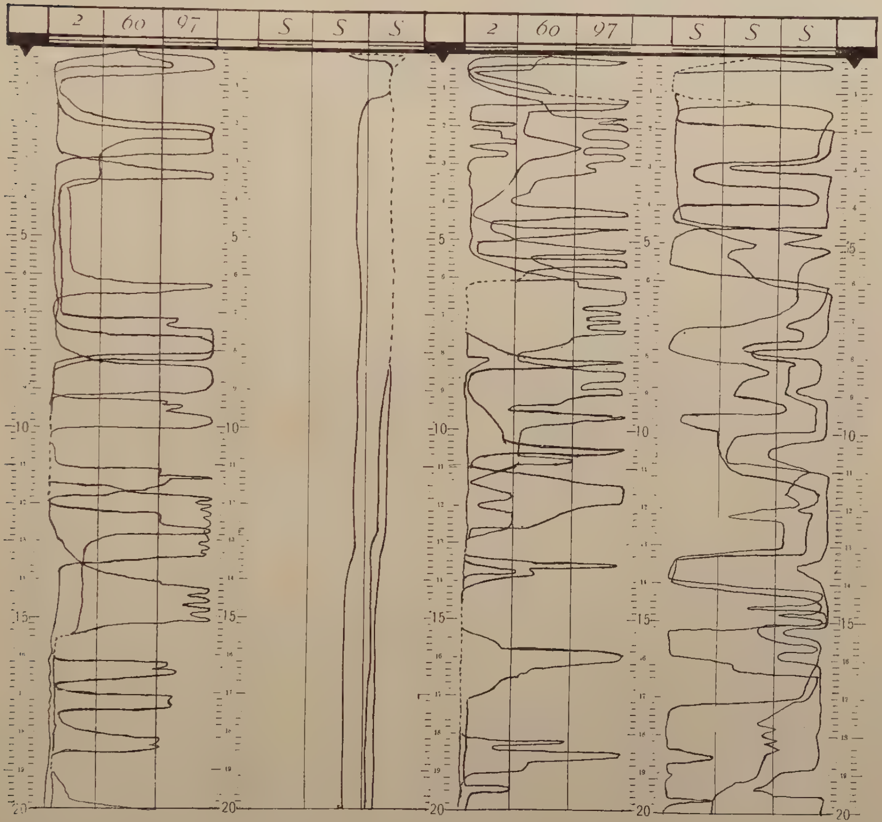


CHART II

Showing modification of the behavior of millipeds (Fontaria) and spiders (Geolycosa) through contact with an evaporation and temperature gradient. The lower temperatures given are for the left and center sections and the higher of the right hand one. For further explanation see Chart I.

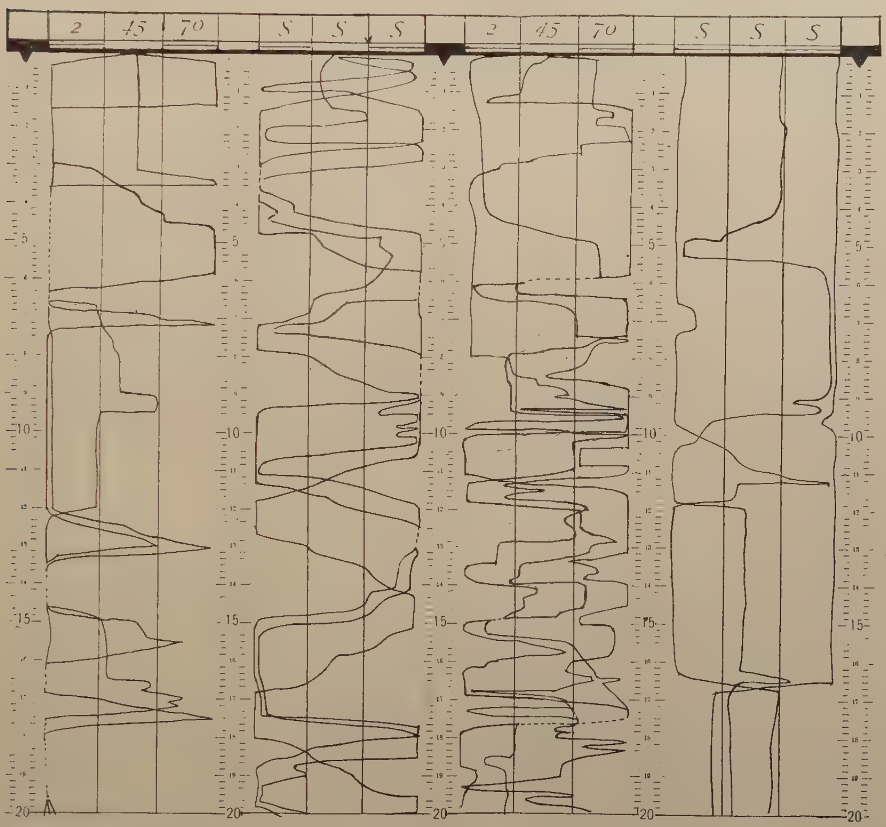
CHART II

FONTARIA—AIR TEMPERATURE
24° and 29°C

GEOLYCOSA—AIR TEMPERATURE
23° and 28°C

Experiment 75 Control

Experiment 79 Control 23°C



which is, I believe, the difference between a graph in which modification of at least one individual is indicated and one in which there is little or no evidence of modification. In Expt. 73, clearly one individual tried air of highest power, then turned back with the second trial, and repeated the same after a brief stay in the moist air. The others appear to have avoided the middle section except for one trial of the air of high evaporating power, after which all came to rest in the moist air. The control of 73, when compared with the rest of the controls indicates the greater activity which commonly occurs in the air that is moving enough to raise the evaporation above the optimum for the animals.

Evidence of modification, as in the case of the fishes (Shelford and Allee, '14), may be of the following types: (a) an animal may begin *turning back* after *entering* the stimulating air a number of times, (b) it may spend shorter and shorter periods of time in the modified air with each entrance; (c) after entering the gradient and turning back in it, an animal may begin to turn back before the change of air conditions is encountered, indicating retention; (d) after having experienced differences in one tank it may remain in one end and turn back from the other when there is no difference between the two ends. The second two types of modification may indicate learning while the first two do not.

Table 1 gives the data on these questions by species and factors. The kinds of experiments in which there was no evidence of modification, are omitted. For example, the experiments with Fontaria and wind gave no good evidence of modification and only experiments with reactions to dry and heated air are included.

Where the reactions were strongly negative the animals sometimes turned back the first time they encountered the stimulating air (Chart I, Expt. 71; Chart III, Expt. 73). All of the species, except Pterostichus which was used for only one experiment, did this when the evaporation was great. Such turnings indicate that the animals sense the strong stimulii the first time they encounter them, i.e., before their sensibility has been increased by repeated contacts with the stimulating air. We note the figures showing the number of times this happened, in the twelfth column of the table. Usually the animals showing modification entered the stimulating air a number of times before beginning

TABLE I

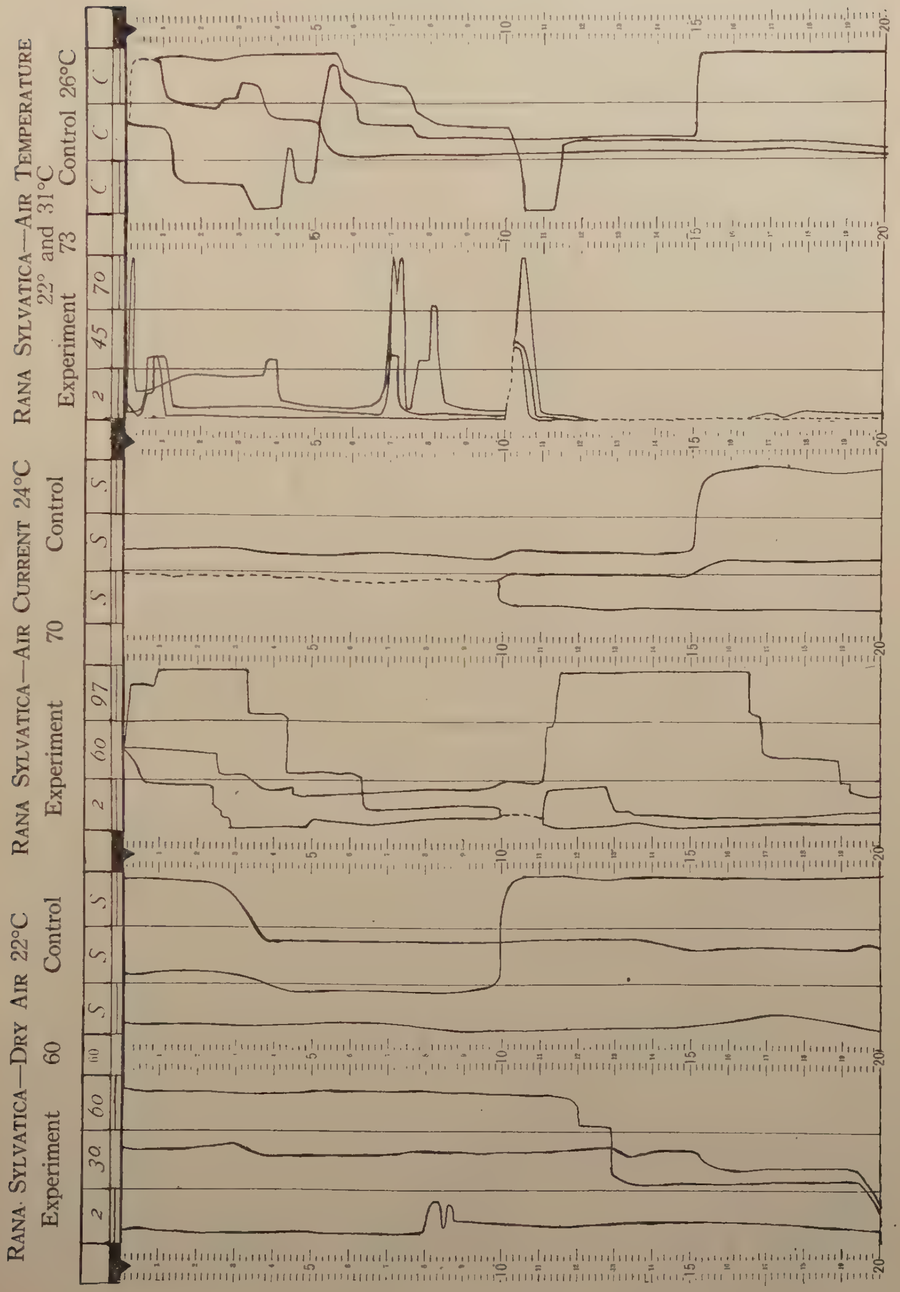
Showing the modification of behavior in the animals studied.

1	2			3	4	5	6	7	8	9	10	11	12	13	14	15
Species	Evaporation			Cause	Temperature	Temperature difference	Number of experiments	Number of individuals	Per cent of individuals showing modification	Average number of trials before modification	Average time in seconds before modification		Reaction		Control	
	L.	M.	H.								Time in lowest evaporation	Time in highest evaporation	Turned the first time	Turned before encountering gradient	Turned before encountering corresponding to gradient	Number of controls
Plethodon cinereus......	.02	.34	.58	Dry air	23	..	6	18	58	1.5	174	41	9	24	14	6
	..	.37	.71	Current	22	..	2	6	66	3.2	575	126.	0	2	2	2
	.02	.35	.58	Heat	22	10	2	6	100	1.6	178	165	1	2	2	2
Averages (a) and totals (t)........................					..	..	t10	t30	a74	a2.1	a309	a111	t10	t28	t18	t10
Bufo................	.02	.34	.76	Dry air	22	..	2	6	100	1.8	338	95	2	2	1	2
	..	.42	1.01	Current	23	..	2	6	100	2.8	168	179	..	..	..	2
	.02	.45	.60	Heat	23	5 & 6	2	6	33	1.0	80	10	2	..	..	2
	.02	.22	.75	Dry air, B.	23	..	1	3	100	2.6	236	278	..	2	..	1
(Not included in totals	.02	.22	.75	Dry air, C.	23	..	1	3	100	1.0	82	88	..	2	..	1
and averages).....	..	..	..	Control, D.	23	..	..	3	100	2.0	236	230	..	..	4	..
Averages (a) and totals (t) of experiments..........					..	..	t7	:21	a 82	a2.0	a205	a141	t4	t4	t1	t6
Fontaria............	.02	.34	.73	Dry air	22	..	4	12	83	2.2	213	85	..	..	..	4
	.02	.37	.76	Heat	22	5 & 10	2	6	83	1.3	527	66	2	..	..	2
Averages (a)and totals (t).......................					..	..	t 6	t18	a 83	a1.7	a246	a75	t2	..	..	t6
Geolycosa............	.02	.32	.18	Dry air	22	..	t 4	t12	a 33	a1.5	a227	208	..	..	..	4
Pterostichus..........	.02	..	.75	Dry air	..	..	t 1	t 3	a100	a2.3	a196	26	..	3	5	1
Average of averages (a).......................					..	..	..	..	93	1.9	236	112	..	..	..	..
Total of totals (t)............................					..	..	28	84	..	..	..	..	16	35	24	27

Chart III

Showing behavior of the wood frog (Rana sylvatica) in evaporation gradients. In the dry air and air current experiments where avoidance of the higher evaporation by stimulation and acceleration is shown. In the temperature experiment modification of reaction is indicated. In control 73 the C's indicate that the air in the control cage was moving. For further explanation see Chart I.

CHART III



RANA SYLVATICA—DRY AIR 22°C
Experiment 60 Control

RANA SYLVATICA—AIR CURRENT 24°C
Experiment 70 Control

RANA SYLVATICA—AIR TEMPERATURE
22° and 31°C
Experiment 73 Control 26°C

to turn back. In the ninth column, we note that the average number of such trials varies from 1 to 3.2 It will be noted, also, in the eighth column that the percent of the individuals tried, which showed modification, varied from 33 to 100. In most of the cases where no modification was indicated, the animals reacted to the higher rate of evaporation from the first or remained in the air of low evaporating power without encountering the higher; hence they do not indicate that the capacity for modification is not present under favorable conditions.

It will be further noted from the tenth and eleventh columns that the length of time spent in the air of low evaporating power is nearly always greater than the time spent in the highest evaporating power (the time spent in the central third is omitted and is usually small).

The experiments were not planned to test the ability of the animals to form associations. In the main, the work was conducted in a manner intended to prevent the formation of associations. There was a considerable stock of most of the animals and in nearly all cases the individuals used in a given experiment were not used again for some days. Still, after the gradient had been encountered a number of times, turning before it was encountered may indicate that the stimulation by the air was associated with the approach to the light or with the screen-covered side on the right (Fig. 1). In the case of *Plethodon cinereus* there were ten more turnings before the gradient was encountered than in corresponding positions in controls and with the exception of *Pterostichus*, the number of turnings in the experiment before entering the gradient exceeded that for the corresponding positions in the controls.

To test the possibility of association formation, four readings (A, B, C and D, Experiments 42 and 43, Chart IV) of the behavior of three toads were made. "A," (Chart IV) is a typical symmetrical control which was observed first. The same toads were then transferred to the experimental cage, and reading begun within five minutes. Here they began showing some avoidance of the air of the high evaporating power at the end of six to eight minutes. At the end of a twenty-minute observation, they were removed for a few (less than five) moments and then returned to the same cage (C) where they showed avoidance of the dry air in *one and two minutes*. At the end of the twenty-minute period (C), the toads were transferred (as before) to the control cage. After a few moments they began to show a preference for the same end that was preferred in the preceding period. While controls sometimes show asymmetry, this is the only one out of ten which shows any such peculiarity.

In the table, the items marked B, C, D, under Bufo, represent two experiments and the control which followed them. In the first experiment (Column 9) the number of trials before turning back was 2.6 and the time over 200 seconds in the highest and lowest evaporation. In the second experiment the trials were reduced to 1.0 and the time to a little more than 80 seconds. In the control observation which followed, they showed a preference for the end corresponding to the moist air with less trials and with less time than was required in the first experiment. Toads have no tendency to come to rest in one end, or in contact with the walls. The two sides of the cage were not exactly alike and the toads could perhaps sense the screen on their right or the lights in front when approaching the end in which the high evaporation occurred in the experiments. The one experiment suggests that the toads may have associated the lights ahead or the view through the screen with the dry air further on (see Fig. 1).

IV. INTERPRETATION OF RESULTS

Protoplasm and the plasmas of organisms possess a definite mechanism for maintaining approximate neutrality. "Neutrality is quite as definite, quite as fundamental and quite as important a characteristic of the organism as its temperature, or osmotic pressure, or in fact anything else we know" (Henderson, '13a). "Within wide limits of amount any acid or base may be poured into the organism and the reaction will not vary," nor will it vary if such be produced by the organism.

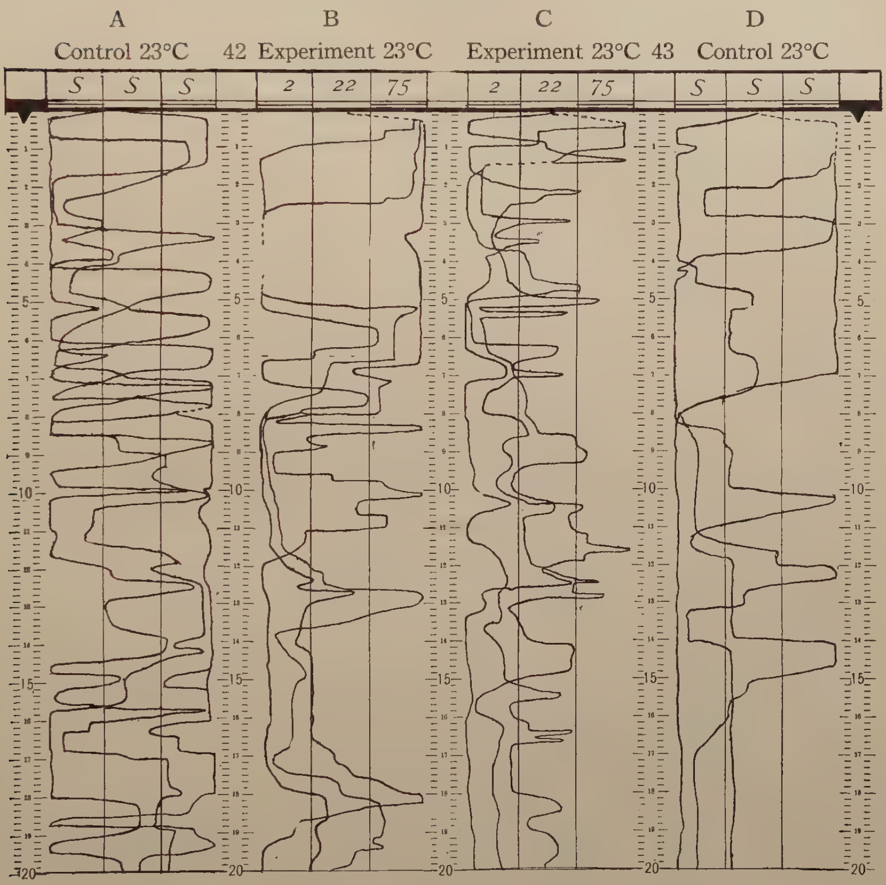
In the preceding paper we noted that presenting acid either externally or internally produced increased sensibility or increased irritability. By this we do not mean to suggest that any particular degree of acidity was probably attained except where staggering occurred, but rather that a tendency toward acidity occurred during the adjustment of the neutrality mechanism. Just what the relation of the ammonia to the neutrality mechanism is in the case of fishes and other vertebrates is not

CHART IV

Showing modification of the behavior of the toads (Bufo) as indicated by experiments following each other closely and by the actions of the toads under control conditions immediately after the second experimental reading was ended.

CHART IV

BUFO DRY AIR—POSSIBLE RETENTION OF MODIFICATION



clear, for while it doubtless causes a tendency to alkalinity, its paralyzing effects are probably due to specific action upon the protoplasm. It should be noted that alkalies, including ammonia, as well as acids, usually excite animals and are almost as potent as acids in causing reversal of reaction (Loeb, '06, Mast, '11), increased irritability, etc. It appears then that a disturbance of neutrality in either the direction of acidity or of alkalinity may be expected to give such results as we have discovered in connection with the reactions of fishes to gradients. The negative reactions here described are to conditions which can primarily either dilute or *concentrate* the *plasma* either in the peripheral sense organs or in the organism as a whole. Did this result in acidity or in alkalinity or did it disturb some other regulatory mechanism? While a probable answer to this question could be presented and discussed, we reserve it until special investigation, now about to be undertaken, may have been completed. It is, however, more than probable that the increased sensibility to air of high evaporating power is due to some disturbance of neutrality, brought about by concentration. We may note, also, that if associations are formed, they go hand in hand with and can hardly be distinguished from the other type of modification. In other words, there is no reason to assume that associative memory is essentially different or stands apart from the type of modification here described. In fact, it appears that since all excitation and all activity increase the output of carbon dioxide the neutrality mechanism may be involved in all associative processes. Henderson ('13a) says it is gradually becoming clear that all physico-chemical conditions in protoplasm—alkalinity, osmotic pressure, colloidal swelling, chemical equilibrium, temperature—are interdependent and that carbonic acid and acid base equilibrium are among all these things probably the most important variable.

Thus it seems probable that many of the simpler problems of associative memory must be referred to the biochemist for solution. The zoologist and the psychologist can by their present methods do little more than describe the phenomena of modification and the best results can come only from general cooperation. The need for cooperation between the psychologist and the naturalist is even more evident than between psychologist and biochemist.

In all of the cases here discussed, except the reactions of the wood frog to dry and moving air, and in most of the other experiments, rapid modification took place. All the stimuli used are those commonly encountered by the animals experimented upon, in their natural environments. It is impossible to determine, however, in the case of animals collected and brought into the laboratory, how much of this ability to avoid disadvantageous stimuli has been acquired during the life of the individual. We note that plants, which respond to environmental changes by variations in growth form, show a similar relation to the various stimuli. Those commonly encountered in nature usually call forth advantageous responses, while those not usually encountered call forth responses which are often decidedly disadvantageous. Here this quality could not have been acquired by the individual in its life experiences and is accordingly to be considered as an innate capacity. It is, therefore, a fairly safe assumption that the capacity to avoid disadvantageous stimuli, and the capacity for advantageous modification, are innate also. Such capacities appear to be common. The difference in the speed with which frogs learn to avoid distasteful food as compared with the time required for them to learn a maze or the presence of a glass plate is a further example of the difference between reactions to natural and unnatural stimuli and problems. As a further example, we note the difference between the apparent "stupidity" of the frog in failing to learn not to snap at a fly when the punishment was the pricking of the upper jaw by a pin or needle (Holmes, '11) as compared with the rapid learning to discriminate between the kinds of food presented when certain kinds brought punishment through the *taste organs* (Schaeffer, '11), the more usual channel for disturbing results of food taking. The raccoon is slow with a man's problem, such as a latch and door problem; what could he do with a forest and hollow tree problem the first time it was presented to him? What could a man do with a forest and hollow tree problem? That with some such problems he errs widely and loses his way often, we are well aware. The use of problems which the animals concerned could never by any possibility have encountered is legitimate, and indeed a necessity if the effect of experience is to be eliminated in animals not bred for experimental purposes. Still, is not the degree of intelligence shown by an animal, with its first problem of a kind common in the experience of the species, a better test of its intelligence in terms of what is so named in our own species, than its ability to solve an entirely unnatural problem ? Why should the intelligence of a monkey be indicated any more by its ability to operate locks, than a man's, by his ability to balance himself upon the swaying branches of a tree ? The comparisons may seem crude, indeed they are so, but the matter in point seems well borne out by the evidence suggested above. The error in rating the intelligence of animals *solely*, *either* upon the basis of problems which they normally encounter in *nature*, *or* those never encountered is not small. Indeed, experimental psychologists have, to a considerable degree, abandoned attempts to rate the intelligence of animals. It is still, however, a common practice among zoologists. To understand the behavior of his animals to the best advantage, the experimental psychologist, should have first-hand naturalistic knowledge of them. The naturalist is even more in need of a knowledge of experimental methods and results. It appears to one not primarily interested in either, that the experimental psychologist should be a naturalist and the naturalist an experimental psychologist.

Theoretically, the explanation of the apparent difference between the relations of animals to natural and unnatural problems is very simple. Direct evidence of recent years tends to show that *natural selection* does not usually, at least, operate upon structural characters in the manner formerly supposed. On the other hand, a rapidly increasingly body of experimental data shows that animals survive or perish under severe conditions in accordance with their irritability and other physiological characters. Irritability is the chief mechanism of survival. Accordingly, where natural selection has been able to operate, responses to stimuli are commonly advantageous; where it has not, they are often disadvantageous and sometimes clearly detrimental.

Two other points are noteworthy. The sensitiveness of the animals used, to slight differences in rate of evaporation shown, makes errors in laboratory experiments easily possible. Air current in controls were practically abandoned because some of the amphibians detected differences in the different parts of the control cage which could not be detected with the hand, making great care necessary in the preparation of each current control. The modification of behavior in gradients here discussed, has been made evident solely by the graphic method of recording the movements of the animals. It is quite possible that application of similar methods to reactions to gradients generally, may show that such modification is the rule, from the more simply organized animals upward.

ACKNOWLEDGMENTS AND BIBLIOGRAPHY

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A GRAPHIC METHOD OF RECORDING MAZE-REACTIONS

ROBERT M. YERKES AND CHESTER E. KELLOGG

From the Harvard Psychological Laboratory

One figure

For nearly twenty years the maze or labyrinth has been employed by students of animal behavior. Both apparatus and procedure have been improved steadily during the last decade, but even to-day we lack an intelligently standardized form of maze and a reliable method of recording the several important aspects of the subject's reaction.

We propose, in this paper, to describe a method of recording maze-reactions which should greatly increase the value of the results obtained in experiments with the maze. We shall not attempt to describe a type of maze which promises to be worthy of standardization, but instead shall limit ourselves to a brief discussion of methods of observation.

Experiments with the maze offer opportunities for the measuring of several aspects of reaction. Especially important among the data obtainable are (1) time of reaction; (2) distance; (3) number of errors; and (4) nature and distribution of errors. Prior to the devising of the method herein described, it has been practically impossible for even the highly practiced observer to obtain accurate measurements of all of these features of reaction. Indeed, with a rapidly moving subject like a rat or a mouse, it has been impossible, during the first few trials, to obtain with accuracy any other measurement than that of time. This is obviously quite as unnecessary as it is unfortunate, for we have good reason to believe that distance and error data are in many experiments more important than time data. Because of our conviction that a variety of data should be obtained in every maze experiment and that all measurements should be made with a reasonable degree of facility and accuracy, we have made it our business to attempt to devise a method which shall enable an experimenter to record the various aspects of reaction directly and graphically.

When the idea of using a graphic method of recording maze-reactions occurred to us, it was immediately suggested, through correspondence, to Professors J. B. Watson and Madison Bentley. The former, feeling the immediate need of such an improvement in the technique of maze experiments, promptly devised and con-

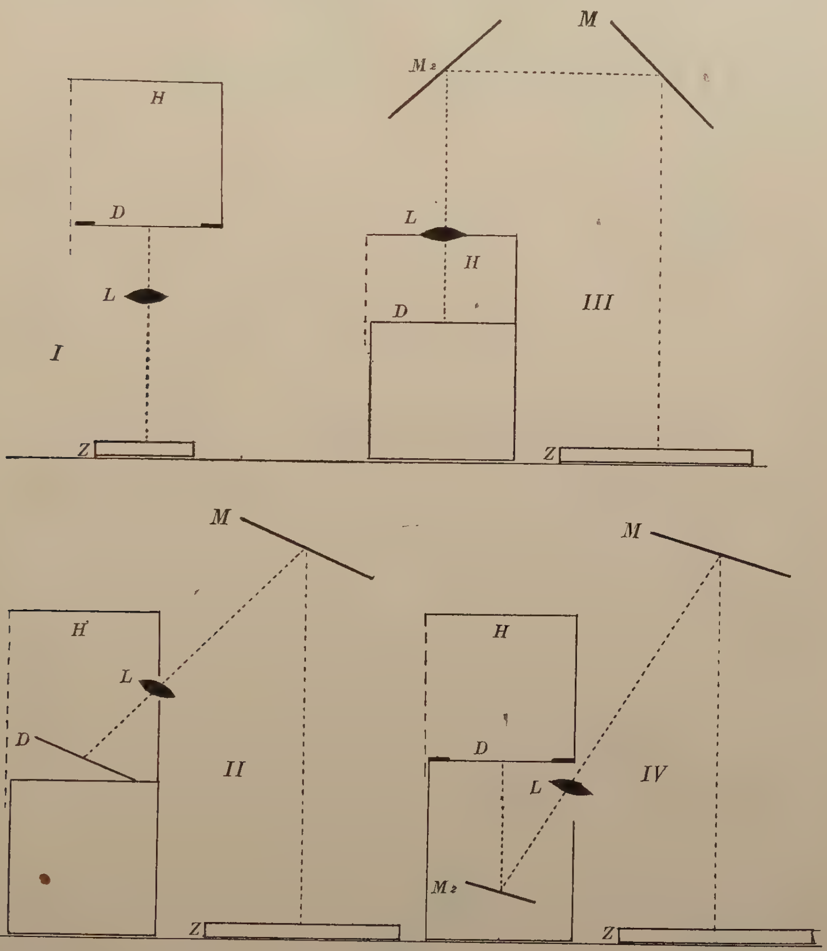

FIGURE 1

Diagrams of four types of apparatus for obtaining graphic records of maze-reactions. I. Apparatus for the direct method: Z, maze; L, lens; D, drawing surface; H, hood. II. Apparatus for simple reflection method: M, mirror. III. Apparatus for double reflection method of Watson: M and M_2, mirrors. IV. Apparatus for double reflection method of Kellogg.

structed what may be termed the camera lucida apparatus. This has been in use for several months in the Psychological laboratory of the Johns Hopkins University and is reported by Professor Watson to work satisfactorily.

In our search for simple, inexpensive, reasonably convenient and adaptable means of obtaining the desired data of reaction, we have happened upon the four methods or devices which are now to be described. Figure 1 is a diagrammatic representation of these several devices. Since they are not of precisely the same value, we shall point out the chief merits of each in describing them.

It was our aim to project, in some convenient manner, an image of the maze and of the reacting subject upon a record sheet which should bear a diagram of the maze. Upon this record sheet the experimenter may accurately trace the path of the animal, while, at the same time, keeping a record of the time of reaction. From the graphic record of the route taken by the animal, the distance and error data may be read.

We shall designate the four methods as the direct method (Fig. 1, I); the simple reflection method (Fig. 1, II); the double reflection method of Watson (Fig. 1, III); and the double reflection method of Kellogg (Fig. 1, IV).

I. *The direct method.* This is the simplest device which we have been able to imagine. Above the maze, Z, of Fig. 1, I, is placed either a simple or a compound lens, L, and at the proper distance above it, a plate of glass, D, conveniently framed in a drawing table, and enclosed by a hood, H. Upon this plate of glass, a thin sheet of paper bearing a plan of the maze is placed. As the observer looks down upon the record sheet, he sees an image of the maze and of the reacting subject, and at will he may trace with pen or pencil upon the record sheet the path followed by the subject.

This method has the important advantages of being extremely simple, inexpensive, and adaptable. It gives a reversed image of the maze, but this is no considerable disadvantage. The chief disadvantages of the method are its inconvenience in connection with large mazes because of the great distance necessary between maze and drawing board. But even with very large mazes, the method may be used to advantage if a vertical distance of twenty to thirty feet is available. This arrangement is likely to prove most practicable where two rooms, the one above the other, are available for maze experiments. The writers have tested the method only with very small mazes.

II. *The single reflection method.* The device for this method, as shown in Figure 1, II, consists of a mirror, M, which is placed above the maze, Z, and which causes an image of the maze to fall upon the lens, L. This image is focused upon a record sheet at D. As in the case of the direct method, the drawing board is hooded in order that the experimenter may work in dim light and thus be able to see, clearly, both the alleys of the maze and the moving animal. In comparison with the former method, this is somewhat more expensive. It yields a completely reversed image and it may be used for even very large mazes. Its chief defects are the inconvenient inclination of the drawing surface, at one end of which the observer must work. In this laboratory we have thoroughly tested the method and find it to work satisfactorily. A little practice enables the observer to follow a rapidly moving rat or mouse and to obtain records which yield accurate measurements of distance, time and errors, even in the early experiments with a given subject.

III. *The double reflection method of Watson* (*camera lucida method*). Two mirrors are used in this apparatus together with a lens and drawing board. The arrangement of these parts is shown in Fig. 1, III. This apparatus has the disadvantage of being more expensive by reason of an additional mirror than the preceding method, and it is also placed at a slight disadvantage because it supplies an image of the maze which is reversed from right to left. To counterbalance these disadvantages, we may mention the following obvious advantages: (1) the more convenient position of the drawing surface; (2) the removal of the experimenter to a considerable distance from the maze; and (3) the adaptability of the apparatus to spatial demands in room or laboratory.

A more detailed account of this method is given by Professor Watson on p. 58.

IV. *The double reflection method of Kellogg.* This differs from method III in that M_2 is placed below the lens, and the image falls upon the record sheet from below, as in method I. Disturbing shadows cast by the hand of the experimenter are thus avoided. The image obtained by this method is completely reversed and the apparatus, as a whole, is quite as adaptable as is Professor Watson's.

General discussion of methods. The above devices for obtaining graphic records of maze-reactions yield less satisfactory results than would a good photographic device, and we recommend them simply because they are less expensive in construction and operation. All are so simple that detailed description is needless. We shall, however, in concluding this article, call attention to certain important points which experience in the use of the graphic method has brought to our attention.

In the first place, although it is perfectly possible to get along with a simple lens, especially if one is working with small mazes, a much more satisfactory image may be obtained by the use of a compound lens. Second-hand portrait lenses are available and wholly suitable, but even such a lens is likely to be much more expensive than a simple lens.

Each of the four devices which we have described has its obvious advantages and disadvantages, and it is clear that choice of a method should depend upon the relative importance of these in each particular case. On the whole, it is likely to be more convenient for most experimenters to have their drawing board slightly inclined toward them. This is possible in methods III and IV. Method II necessitates the use of an inclined drawing board, but unfortunately the observer must sit at one end of this board and work in a somewhat awkward position. So far as the position of the drawing surface is concerned, methods III and IV would seem slightly more satisfactory than methods I and II.

In those devices in which the light falls upon the record sheet from above, the shadows cast by the experimenter's hand and pencil are disturbing, sometimes rendering it difficult to follow accurately a swiftly moving animal. Other things being equal, it is therefore preferable to have the light come from beneath the drawing surface, as in methods I and IV.

In the first few trials with a given animal, it is extremely important for the experimenter to be able to change record sheets quickly, since the animal is likely to traverse the alleys of the maze rapidly and repeatedly. If the image comes from above the record sheet, it is possible to have the sheets made up in the form of a tablet or block with two edges glued. The tablet having been properly oriented, the experimenter may at any moment tear off a record sheet and continue his tracing almost uninterruptedly. This method may be made to work satisfactorily even when a printed diagram of the maze appears on each record sheet, for the orientation of the block may be kept constant. When the image falls upon the record sheet from below it is necessary to use rather thin paper and to have the drawing board so arranged that the sheets fit neatly and may be quickly placed in position. Although we have tried only methods I and II in this laboratory, we are inclined to believe that it is more satisfactory on the whole to have the image come from below the record sheet. Especially in the first trials with a given animal, the time required is likely to be long, and the experimenter should be able to make his observations without undue discomfort or fatigue.

We recommend that as soon as the experimental device has been selected and properly adjusted, a zinc etching, which exactly reproduces the image of the maze as it falls upon the drawing board, be made, and that this be used in the preparation of blank record sheets. For, although a diagram of the maze is not absolutely essential, it has considerable value in connection with the early trials and sometimes prevents errors in the reading of records of later trials. It is extremely laborious and wasteful of time to draw the diagrams by hand, and if hundreds or thousands of record sheets are to be used, the cost of a zinc etching and of printing the sheets will be trivial in comparison with the value of the experimenter's time.

As appears from the above discussion, we are not in a position to recommend any one of the four methods over the others without careful consideration of the type of maze which is to be used, of the character of the lens, and the location of the apparatus. But we are fully convinced that all investigations with the maze should make use of some graphic method of recording reactions. There can be no doubt that the data previously obtained from maze experiments have only a fraction of the value which they should have, and that because of the inaccuracy and incompleteness of the records.

A CIRCULAR MAZE WITH CAMERA LUCIDA ATTACHMENT[1]

JOHN B. WATSON

The circular maze shown in Fig. 1 is made with wooden base and aluminium walls. The base is 150 cm. in diameter and 4 cm. in thickness, and is constructed as follows: Two wooden discs 150 cm. in diameter and 2 cm. in thickness are first sawed out. These two discs are finally glued together. Before glueing, however, the upper disc is marked off into a series of concentric circles. The diameter of each of the circles is as follows, beginning with the outermost one: 140 cm., 120 cm., 100 cm., 80 cm., 60 cm., 40 cm., and 20 cm. These circles are then sawed out upon a band saw. The width of the saw is so chosen that it is just equal to or slightly larger than the thickness of the aluminium sheets used for the walls. After sawing, the disc as a whole is converted naturally into a series of concentric rings. These are fastened down to the lower disc with hot glue and screws. The lower surface of the base is thus solid, while the upper surface shows a series of grooves into which the aluminium walls may be slid. Soft aluminium bought in rolls is used for the latter. The height of the aluminium is 18.5 cm., the thickness, .8 mm. The aluminium is unrolled and cut into the proper lengths. Each strip is cut just 10 cm. shorter than the length of the circular groove into which it is to be fitted. This gives an opening into the alley. By means of this arrangement it is possible to slide the aluminium around in its groove and thus to place the entrance in any desired position. Fig. 1 shows clearly the construction of the maze, the number of alleys, the placing of the entrances, and the radial stops.[2]

This maze offers several desirable things in work of this character: in the first place it can be used on the unit plan, in that only the home box and the surrounding segments need be

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[1] From the Psychological Laboratory of The Johns Hopkins University.

[2] The base as a whole may then be sawed into half or quarter sections for convenience in shipping or storing. Indeed, it is easier to build the base in half sections. When set up the sections are locked together and placed horizontally upon a wooden framework. The material should be well seasoned. A thorough coating of boiled linseed oil should be applied.

used where a very simple maze is desired. The addition of other segments then merely increases the complexity in an, at present, unknown ratio. The coefficient of increasing complexity could be determined by allowing one group of animals to learn the maze in its simplest form, another in its next most complex, etc.

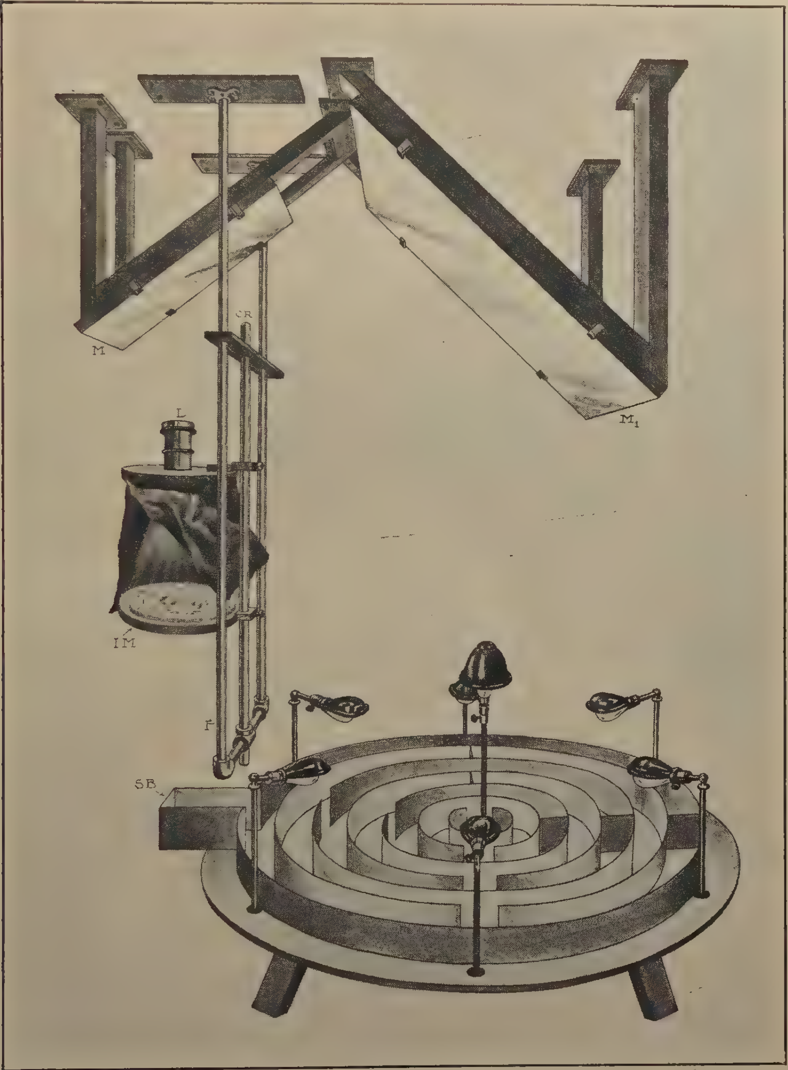

FIGURE 1. General view illustrating camera-lucida maze

Secondly, the ease with which complications can be introduced makes the maze very desirable. This is brought about by the flexibility in the arrangement of the entrances and radial stops. Fig. 1 shows the maze just as it was used by Miss Hubbert in the work which she reports on page 60.

The camera lucida attachment is easily installed; it is simple and permanent. Had it not been for Professor Yerkes' insistence upon the necessity for having some recording device for the movements of the animals, it is doubtful if this attachment would have been made in its present form. He suggested to me two years ago that some such device would be desirable and that he had certain plans for its construction. Before the publication of his work it became necessary to have an exact record of the stages of the acquisition of the maze habit, since Miss Hubbert wished to undertake a comprehensive study of the difference in the acquisition of habits of animals of different ages. Accordingly, I went ahead independently and finally constructed the apparatus which is shown in Fig. 1.

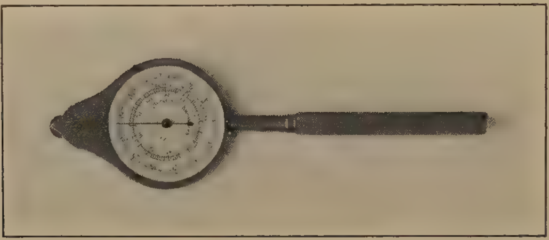

FIGURE 2. Chartometer

A large plate glass mirror (M_1), 91 cm. wide by 121 cm. in length, was placed at an angle of 45° directly over the center of the maze. This mirror was strapped by small clamps to the edge of the supporting framework. At a certain distance from this mirror a second mirror (M), 60 cm. by 75 cm., is placed at an angle of 45° above the maze and at such a distance from M_1 that the light reflected downward from M falls outside of the maze. Below M, and in the path of the light reflected from it, is placed a single achromat (L), 6 cm. in diameter and 50 cm. focus. The lens is placed in a barrel and the barrel is attached to a wooden disc 30 cm. in diameter. This board is attached to an iron collar which slides freely up and down the rod CR. This gives a very easy means of adjusting the size of the image, focusing, etc. Below this first disc will be found a second disc similar in character and controlled in the same way. A pad of circular paper is laid upon this disc.[3] A reduced image (IM) of the maze appears upon this paper. Extraneous light is excluded by means of a soft black flannel curtain attached to the disc which supports the lens (L). As may readily be seen from the figure, the maze must be illuminated quite highly in order to produce a clear image. The illumination is obtained by means of six lights placed symmetrically around the maze and by one light in the center of the maze. The six lights on the periphery are supplied with opaque half shades, the light in the center of the maze with a similar opaque circular shade. These shades are of aluminium, blackened on the upper surface. The floor of the maze is covered with imported white linoleum. This serves to reflect the light upward to M_1, thence to M. Passing through the lens the rays are brought to a focus at IM. The ratio between the maze and the image is 6.4 to 1. The image appearing at IM is extremely clear when proper precautions are used to sensitize the eye. Even the smallest mouse can be seen quite clearly.

The movements of the animal are traced upon white paper with a soft pencil. In the early stages of learning several sheets of paper are used on each animal at any given trial in order to avoid a too complicated tracing. Each sheet is marked with the number of the animal, the number of the trial and the serial number of the tracing. The length of the lines so traced is measured by means of a chartometer furnished by Eugene Dietzgen and Co. Keuffel and Esser furnish a similar and somewhat better instrument. This instrument is surprisingly accurate even in measuring lines which are tortuous in their course. The error in measuring the length of the charted lines is about one per cent. Fig. 2 shows the chartometer actually employed.

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[3] It is convenient to cut out several sheets upon a disc cutter and to stamp a hole 13 mm. in diameter in the center of each for the reception of a stud 13 mm. in diameter and 1 cm. height placed in the center of the board IM.

TIME VERSUS DISTANCE IN LEARNING[1]

HELEN B. HUBBERT

The present investigation is concerned with the factors of the total time consumed and the total distance run in the learning of the maze by rats. The maze used in obtaining the records presented below was designed by Professor Watson. He describes the maze elsewhere in this issue of the Journal (p. 56).

The records were taken in terms of the time consumed in running from the point of entrance to the food box, and of the total distance traversed during this time. Timing was done by means of a continuous stop-watch registering one-fifth seconds. The watch was started the moment the animal left the starting box (S. B., Fig. 1, p. 57) and was stopped at the moment of entrance into the food box in the central compartment of the maze. The distance record was obtained by tracing the movements of the rat upon soft white paper with a very soft pencil. The tracing so obtained was then measured by means of a chartometer which had been calibrated. Calibration showed that the instrument had an error of about one per cent. As has been stated by Professor Watson, the ratio of the size of the image to that of the maze is as 1 to 6.4. Consequently, the distance in cm. obtained with the chartometer must be multiplied by 6.4 in order to obtain the actual distance run by the animal. The values given in the table represent the actual distance covered by the rats. For example, in trial 31 (p. 163), the distance accumulated by the chartometer was 92.69 cm. Converting this we have 92.69 cm. x 6.4=593.2 cm., as the actual distance run. Figure 2 shows the actual tracing, figures 1 and 3 the diagrammatic representation, of the paths traversed by two rats in the trials indicated.

The records of the total time consumed (T.) and of the total distance (D.) run were taken on 27 rats, 14 males and 13 females. The animals began the problem when 35 days old. They were born and reared in the laboratory, consequently all were tame and accustomed to handling. The rats had been fed in the maze

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[1] From the Psychological Laboratory of the Johns Hopkins University.

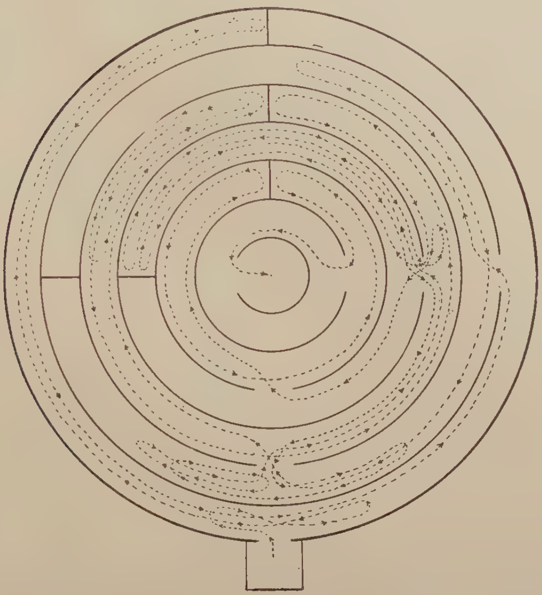

FIGURE 1. Schematic representation of pathway traversed by rat No. 28 on his 2nd trial in the maze. Four sheets were used in the actual tracing. Time, 2419.8 seconds. Distance, 1579.2 cm.

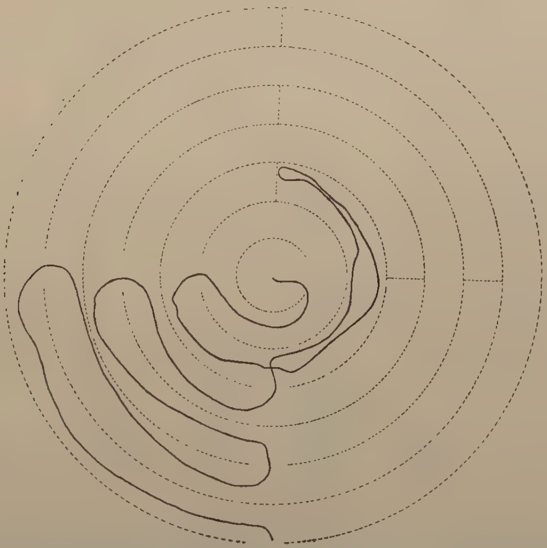

FIGURE 2. Actual pathway traversed by rat No. 26 on the 62nd trial in the maze. Time, 31 seconds; Distance, 630.4 cm.

for a week before the experiment began, but during feeding they were strictly confined to the food box.

Two trials per day were given each rat, and at the end of the second trial the animal was allowed to eat in the food box for from three to five minutes. Milk-soaked bread was used as the incentive throughout. Until the animals were 45 days old they were allowed to eat food in the cage for from three-quarters of an hour to one hour after each day's run. The rats were run every day and as nearly as possible at the same hour every day, since it was found that rats accustomed to being run at night did not react well if forced to run in the daytime.

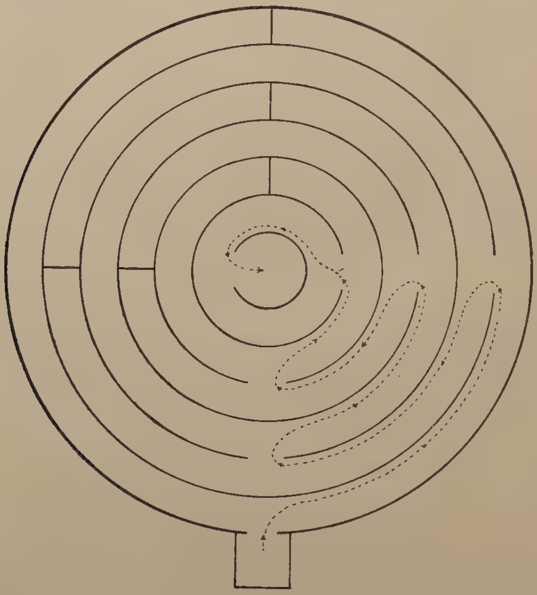

FIGURE 3. Schematic representation of pathway traversed by rat No. 26 on the 78th trial in the maze.
Time, 5.8 seconds. Distance 448 cm.

The problem was considered learned when the rat, for six consecutive trials, went straight to the food box without stopping or turning aside from the true pathway, i.e., when all excess movements had been eliminated. No time limit was set, but as a matter of fact it was found that most of the rats made such runs in six seconds or less. The shortest perfect run was 4.2 seconds,

TABLE 1

Trial No.	No. Rats Running	Average Time	Average Distance cm.	Trial No.	No. Rats Running	Average Time	Average Distance cm.
1	27	467.0	4216.1	59	18	15.9	607.7
2	27	627.7	3736.1	60	18	10.6	550.9
3	27	413.8	3147.8	61	18	10.1	519.5
4	27	158.5	1866.9	62	18	9.9	558.0
5	27	129.9	1573.6	63	18	14.5	553.5
6	27	186.6	1719.2	64	18	12.9	581.3
7	27	79.2	1164.1	65	18	10.1	551.7
8	27	68.8	1300.2	66	17	8.4	518.2
9	27	48.1	925.6	67	16	10.5	562.2
10	27	64.9	1169.0	68	16	8.8	505.0
11	27	40.3	1029.8	69	16	6.6	473.4
12	27	62.9	1240.7	70	16	22.5	496.6
13	27	59.4	925.1	71	15	7.7	484.3
14	27	77.7	1022.5	72	15	8.4	489.4
15	27	86.9	874.6	73	15	8.7	518.0
16	27	25.5	868.4	74	14	18.4	519.3
17	27	20.8	671.5	75	11	12.9	416.0
18	27	51.0	1148.1	76	10	26.5	526.7
19	27	33.1	772.0	77	8	11.2	480.8
20	27	35.4	1032.7	78	6	44.6	706.1
21	27	24.2	739.9	79	5	42.3	798.7
22	27	48.2	1010.4	80	5	36.4	508.2
23	27	19.6	649.5	81	5	8.6	448.0
24	27	24.5	789.0	82	5	147.7	788.5
25	27	27.7	754.7	83	4	28.1	600.0
26	27	26.1	756.5	84	4	359.8	1468.8
27	27	71.6	776.6	85	4	55.9	794.4
28	27	16.9	633.3	86	4	6.6	451.2
29	27	36.7	641.9	87	4	19.7	513.6
30	27	25.1	790.8	88	4	6.3	448.0
31	27	31.8	593.2	89	4	13.9	556.8
32	26	25.1	734.8	90	4	7.4	526.4
33	25	100.5	830.5	91	3	47.7	780.8
34	25	30.3	821.6	92	3	15.8	669.9
35	25	19.6	559.5	93	3	24.1	805.3
36	25	31.2	840.5	94	3	6.1	448.0
37	25	19.9	520.6	95	3	52.2	1339.7
38	25	20.5	674.1	96	3	7.2	509.9
39	25	27.3	569.6	97	3	24.7	904.5
40	25	28.9	879.7	98	3	7.0	448.0
41	25	57.3	704.0	99	3	10.1	460.8
42	25	18.2	616.7	100	3	6.1	460.8
43	25	9.0	505.0	101	3	6.9	448.0
44	25	13.7	603.8	102	3	5.3	448.0
45	25	12.3	497.5	103	1	11.2	448.0
46	24	19.0	716.4	104	1	5.4	448.0
47	23	37.1	683.4	105	1	8.0	537.6
48	23	14.7	574.3	106	1	4.8	448.0
49	22	24.1	581.2	107	1	8.0	448.0
50	22	24.4	706.5	108	1	12.0	566.4
51	21	15.7	534.3	109	1	5.2	448.0
52	21	12.6	514.7	110	1	5.4	512.0
53	20	14.1	521.6	111	1	5.4	448.0
54	20	9.9	500.8	112	1	5.2	448.0
55	19	8.4	506.8	113	1	4.2	448.0
56	19	13.3	545.2	114	1	4.8	448.0
57	19	19.6	588.3	115	1	5.8	448.0
58	19	10.4	562.5	116	1	4.0	448.0

the longest, 14.2 If a rat remained in the maze for 15 minutes without reaching the food box he was taken out and replaced in the entrance box for a second attempt. Distance and time were recorded in the same way as for a successful run, i.e., when an animal worked for 15 minutes on his first trial, and failed, and then attained success after eight minutes on his second attempt, the total time of his first trial would be 23 minutes. Distance was treated in a similar way.

In the Table 1 given above, the time record and distance record of all individuals at work upon the problem at any given trial were separately averaged, e.g., in trial 1, 27 animals were used, the time and distance records were taken and then averaged separately, giving one point on the time curve and one on the distance curve respectively. Once the problem had been learned by an animal it was taken from the group. As may be seen in Curve 1, plotted from Table 1, the number of animals at work is steadily decreasing.

The striking similarity between the time and distance curves bears out the contention of Watson and of Hicks that the time record is a good index of progress in learning. It will be recalled that this position has been severely criticised by Washburn[2] and by Yerkes[3]. The similarity of the curve contour, and the close correspondence of the maxima and minima is apparent. As Hicks has pointed out, certain differences between T. and D. appear in the early trials. The drop in time in the first nine trials is 89.5 per cent, while that in distance is 78.5 per cent. A partial explanation for the increased percentage of the time drop may be found in the rat's behavior during the first few runs in the maze, when he often crouches against some partition and refuses to run for three, six, ten and sometimes even fifteen minutes. In such cases the *time* average increases enormously, while the distance average remains practically unchanged. Perhaps a better method of procedure would have been to deduct from the time record the time spent in absolute quiet, but this would lead into difficulties of standardization, making necessary an arbitrary decision as to how much time shall elapse without movement on the part of the rat before deduction is justifiable—a pitfall similar to that encountered in computing *errors*, and one we are anxious to avoid. It is this same system of taking records, however, which largely accounts for the apparent discrepancy in the time curve from the 81st to the 86th trial. Rat No. 22 became erratic, increasing his time record enormously here, while his distance record changed but little. Thus in the 82nd trial, where the first decided rise occurs, his time record was 715 seconds, while the combined time of the other rats running was only 23.6 seconds. Had No. 22 not been running the average time would have been 5.9 seconds instead of 147.7 seconds, while the average distance would have been 448 cm.

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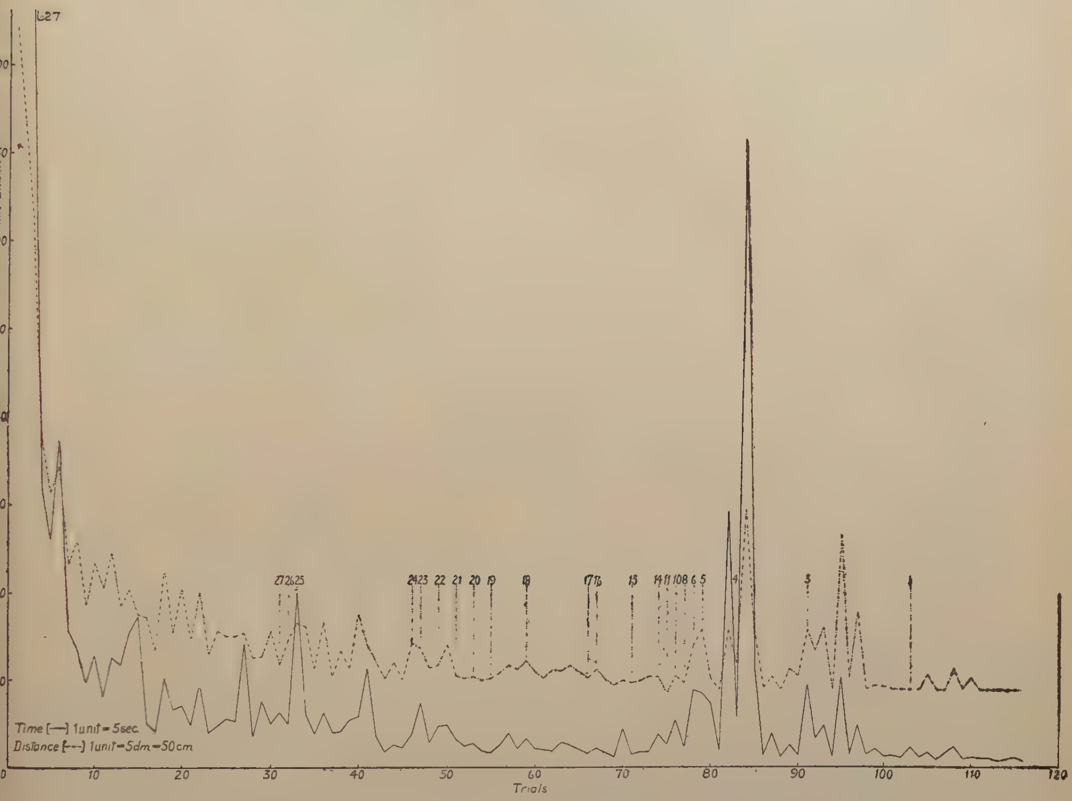
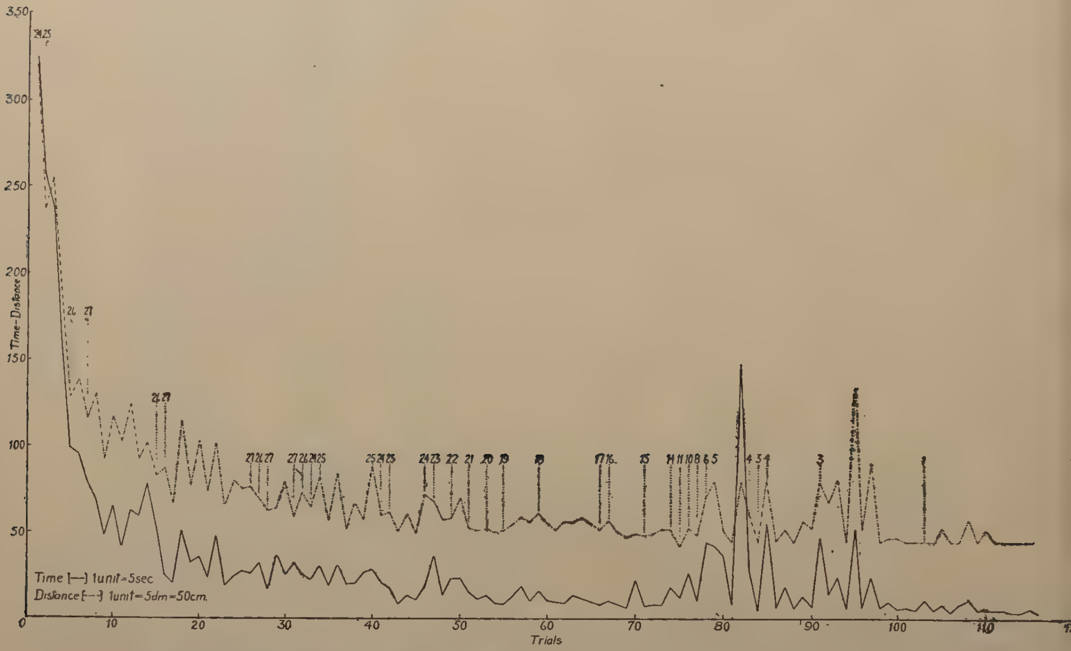
[2] Washburn, M. F., *Jour. Comp. Neur. and Psy.*, 1907, Vol. 17, p. 532.

[3] Yerkes, Robert M., *Jour Phil., Psy. and Sci. Methods*, Vol. IV, p. 585..



Curve I. Relation of time to distance. The figures above the curve indicate the number of rats running at each trial. Failures are counted in. The first point in the time curve is 350, the second (not shown in curve) 627. Plotted from the figures in Table 1.

instead of 788.5 cm.[4] So in the 84th trial. Here the recorder's note-book states that after the first spurt, which occupied a little over two minutes, the same rat, No. 22, refused to run and crouched near the far partition in alley 1 for the remainder of the 15-minute norm. Again throwing out his record, we have a time average of 5.3 seconds instead of 359.8 seconds and a distance average of 4,480 cm., instead of 1,468 cm. In the 86th trial, he steadied down and the throwing out of the record here gives 5.4 seconds instead of 6.6 for time and 452.3 cm. instead of 45.1 cm. for distance. The small curve, Curve III, shows the effect of throwing out the record of rat No. 22. The similarity of the time and distance curves again becomes apparent. An additional factor which must be considered in respect to both time and distance, when interpreting the latter part of Curves I and II, is the small number of rats then running. The best ones had dropped out



CURVE II. Plotted from Table 2, which is the same as Table 1, except that failures are eliminated.

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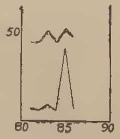
[4] It will be remembered that the minimum time may be taken as seven seconds while the minimum distance is 448 cm.

and at the 81st trial only five were running, while at the 86th trial only four remained. Where only a few animals are running individual differences are sure to alter the curve contour.

With the exception of the discrepancy shown in the first eight trials and the apparent discrepancy in the final trials, the time and distance curves show great similarity in contour.

Table 2 shows the effect of throwing out both time and distance records in each case of *failure* on the part of individual animals. It was found that the figures were identical with those of Table 1, except for the trials indicated. For the sake of comparison the original records (Table 1) for the corresponding trials are repeated. Examination of Curve II, plotted from these figures, shows a somewhat steadier curve and in general a closer approximation between time and distance. The same explanation which was offered in the case of Curve I for the discrepancy from the 81st to the 86th trial holds here.



Curve III. To show the effect of eliminating the records of Rat No. 22 from the 81st to the 86th trial.

TABLE 2

Trial No.	Failures Averaged			Failures Eliminated		
	No. Rats	Average Time	Average Distance cm.	No. Rats	Average Time	Average Distance cm.
1	27	467.0	4216.1	24	325.7	3203.2
2	27	627.7	3736.1	25	257.1	2373.9
3	27	413.8	3147.8	25	236.9	2553.7
5	27	129.9	1573.6	26	98.4	1279.7
6	27	186.6	1719.2	26	95.3	1379.7
15	27	86.9	874.6	26	53.3	822.7
27	27	71.6	776.6	26	32.4	700.5
33	25	100.5	830.5	24	23.0	648.0
41	25	57.3	704.0	24	20.3	595.1
84	4	359.8	1468.8	3	5.3	448.0

In an admirable discussion of the values of curves of learning[5] Miss Hicks says (p. 141): "The total distance criterion presents so many difficulties as to render it impracticable for ordinary work. One difficulty lies in the matter of taking records accurately. The rats, after a few trials, run so rapidly that it is extremely difficult for one person to observe and record at the same time. To do this, it is necessary to mark off the maze into small segments and commit to memory some scheme of representation so that records can be jotted down in a purely automatic manner. The work of transcribing this record into distance terms and computing the same is very laborious. *Eliminating these practical difficulties, the distance criterion is in some ways an ideal one.* (Italics mine.) There can be no divergence of practice as to what shall be omitted or included and results obtained by different experiments upon the same maze will be strictly comparable." (Page 154.) "The distance and error criteria are fundamentally alike. The distance curve is the better representative of the progressive approximation of the act towards automatic accuracy. It portrays all the details of this eliminative process and it approximates the ideal of uniformity and regularity of descent. However, it is impracticable from the standpoint of recording and manipulating the data."

These practical difficulties in recording and manipulating the data have been overcome, at least where small animals are the subjects used in the maze. The total distance record can be obtained accurately. Its desirability has, so far as we know, never been questioned. The error curve has often been used in lieu of the distance curve, but it has been criticized as practically valueless because of the difficulties encountered in standardizing an "error."[6] "The prevalent practice of omitting all total and partial returns from the error record, and of making no attempt to evaluate varying degrees of error gives a curve which is not only worthless but false."[7]

With this criticism on the customary methods of obtaining the errors committed by an animal we are in hearty sympathy. It is far better, both from the standpoint of convenience and that of accuracy, to base comparisons upon the time alone than to consider these so-called errors. As to which type of record is best, time or distance, it seems wise to await a more complete study of the question before deciding.

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[5] Hicks, V. C., The relative values of the different curves in learning. *Jour. Animal Behav.*, Vol. 1, pp. 138–156.

[6] Watson J. B., The behavior of noddy and sooty terns. *Carnegie Pub.*, No. 103, p. 249, note 1.

[7] Hicks. Ibid., p. 156.

CONCLUSIONS

I. It is possible to chart the path of the run of an animal through the maze and to measure accurately the total distance covered in that run.

II. Time and distance curves are so similar in character when normal animals are tested that it is impossible to state which is the better criterion of learning. We are sadly in need of a close analysis of just what time and distance curves mean. In determining the activity at different ages, the difference between blind and normal animals, between anosmic and normal animals, etc., there still remains the possibility that the distance and time curves will show great disparity. It is not fair, however, to maintain this until there is some factual evidence in its favor.

ON SOUND DISCRIMINATION BY CATS

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This paper is a report of experiments which were made on cats, to ascertain their ability to discriminate sounds; viz.: differences of musical notes of different pitch, and differences of intensities of " noise." If an animal forms an association between a certain musical note and food, so that he reacts in a definite manner to that note in order to obtain food, and does not so react to other notes, we may infer that he discriminates that note from the other notes. In a similar manner a cat may give evidence that it distinguishes one " noise " from another " noise " of a different intensity.

Kalischer[1] has reported experiments with dogs on auditory discrimination, in which his animals showed ability to discriminate pitch. His method was to sound a certain note on an organ, or on an harmonium, whereat the dog should react in a definite manner, such as by springing up and snapping at a piece of meat which the experimenter held out in his hand. Selionyi,[2] using the " Pawlow method " on dogs, obtained evidence of discrimination by them of the tones of an organ, of organ pipes, and of the sounds of two whistles. Selionyi, as well as Kalischer, was chiefly interested in sound discrimination from a physiological standpoint. In experiments on auditory discrimination in raccoons made by the present writer, reported by Cole,[3] evidence of discrimination of musical pitch by these animals was obtained. In experiments which I made in 1909 on auditory discrimination in Rhesus monkeys, satisfactory evidence of discrimination by the latter animals of pitch, and also of " noise," was obtained.[4] Johnson,[5] in tests on sound discrimination in dogs, lately made at the Johns Hopkins University, got some positive results. However, I am informed in a verbal report of the experiments by Dr. J. B. Watson, that an average of only about 60 per cent. of correct responses was obtained.

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[1] Kalischer, O., Eine neue Horprufungsmethode bei Hunden. *Sitz. d. Kgl. Ak. d. Wiss.*, X, 1907, 204 ff.

[2] Selionyi, G. P., Contribution to the study of the reactions of the dog to auditory stimuli. St. Petersburg, 1907.

[3] Cole, L. W., Concerning the intelligence of raccoons. *Jour. Comp. Neur. and Psy.*, **17**: 236.

[4] Shepherd, W. T., Some Mental Processes of the Rhesus Monkey. *Psy. Rev.* Mon. Sup. No. 52, 1910, 26 ff.

[5] Not published at this writing, Dec. 17, 1912.

At the time the experiments herein reported were begun, one of the animals was eighteen months old. Its only previous training had been in some tests on discrimination of articulate sounds, completed about nine months previously to those experiments. The animal appeared to be of medium intelligence. The other cat, the mother of the first, was about four years old. It had received the same training in sound discrimination as the other animal, and at the same time. The latter cat was of average intelligence. Both were ordinary grey house cats.

In the experiments on pitch discrimination to be reported in this paper, I used the same plan as I had employed in the experiments with the raccoons and with the monkeys, and which is somewhat similar to the method Kalischer employed. The cat was placed in a cage 66 centimeters in height. A wire netting formed the front, and also the top of the cage. The experimenter sat at a distance of about a meter from the cage and sounded a certain note on the instrument used. At this note, in the case of the first animal, Pet, the cat was to rear up with its paws on the front of the cage and look ~~up~~ through the top of the cage for food to be given it. At the other notes, it was not so to react. In the case of the second animal, Mary, on account of its inactive habits, as shown in previous experiments, it was deemed a sufficient response if it merely looked up at the top of the cage for food, when the "feed" note was sounded. But whether or not a positive response was obtained, the animals were fed when the "feed" note was sounded. Ten seconds were allowed for a response. In experiments 1 and 2, an ordinary harmonica, A, was used; in experiment 3, a Bradbury piano; the procedure in experiment 4 will be explained under that head. In each test, care was taken not to give by looks, movements of the hands, or in any other manner, any cue to the proper response. In order that the animal might not react to the mere rhythm of the sounds, they were sounded in an irregular order.

1. Discrimination of a Difference of Two Octaves of Pitch on a Harmonica. A-3, Food Note; A-1, Non-food Note.

Pet.—In the first day's experiment, this animal showed indications of forming the association; in thirty trials[6] it responded to A-3, the food-note, fourteen times, and to A-1 two times. Its first correct reaction was in the eleventh trial, the next in the twelfth, next the fourteenth, then the seventeenth, and in an increasing degree throughout that day's tests. On the second day, in fifteen trials, or in forty-five trials in all, Pet had perfected the association. In fifteen trials on that day it responded to A-3 fourteen times with one doubtful response, and to A-1 one time with three doubtful. In two trials that day, the fourth and the seventh, the animal got up at A-1, but got down at once and appeared, from its looks and actions to know that it had made a mistake. In ten test trials four days later, the cat reacted to A-3 ten times and to A-1 none.

Mary.—The older animal showed no definite indication of forming the association until the third day. On that day, in ten trials, it responded to A-3 eight times and to A-1 five times with two doubtful responses. After this, Mary continued to improve, and on the seventh day had perfected the association. In twenty trials that day, or in ninety trials in all, the animal responded to A-3 nineteen times, and to A-1, five times, with two doubtful. At the twentieth trial, when I sounded A-1, Mary went to " washing her feet," and appeared, by her actions, to know that no food was to be gotten at that note. In two additional day's tests, Mary responded to A-3 twenty times in twenty trials each day, with five and four wrong responses respectively on the eighth and ninth days. This cat never entirely inhibited the tendency to react to A-1.

2. Discrimination of a Difference of One Octave of Pitch. Notes A-2 and A-1 on a Harmonica. Fed at A-2.

Pet.—In the first day's experiment, in ten trials, the animal gave no positive response. I had handled it rather roughly on the previous day, and the cat appeared uneasy and afraid of me. Also it did not seem hungry. On the following day, in twenty trials, or in thirty trials in all, Pet reacted to A-2 eighteen times and to A-1 two times. It did not respond to A-2 in the first trial nor in the eleventh. The animal reacted to A-1 (wrong) in the third and fifth trials only. When it got up at A-1 in the fifth trial, it *got down at once*, and gave every indication of being aware that it had made a mistake. In a test of ten trials on the following day, Pet made no mistakes.

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[6] That is in thirty trials of each auditory stimulus.

3. Discrimination of the Difference of Two Octaves of Pitch on a Piano; i.e., between F-1, Bass Cleff, and F-2, Treble Cleff. Fed at F-1. Not fed at F-2.

Pet.—On the first day of this experiment, in twenty trials, the cat reacted to A-1 thirteen times and to A-2 three times. Its wrong responses to A-2, were in the first, second and fifteenth trials. On the second day of the experiment (three days later), in twenty trials, or with forty trials in all, Pet responded to A-1 twenty times and to A-2 none. In the first trial on that day, the animal got up *slowly* at the food-note, as if in some doubt what to do. In the remaining nineteen trials correct responses by the cat were prompt.

4. Discrimination of Noise.

The animal was placed in the cage as in the preceding experiments on pitch discrimination. The sound apparatus consisted of a wooden box, 18 x 11 x 10 inches, and a slat 13 x 4 x $\frac{5}{12}$ inches, fastened to the top of the box by a leather hinge. By raising the free end of the slat and suddenly letting it go, it struck the top of the box and made a sound varying in loudness with the force with which it struck. To give sounds of different degrees of intensity or loudness, two sticks, one 2½ inches in length, the other 4½ inches, were separately used and placed perpendicular to the box, under the free end of the slat. By pressing on the slat near the hinge and suddenly removing the shorter stick, the slat would strike the box and produce a sound of noticeable intensity, and by using the longer stick in a similar manner, a louder noise was made. The same pressure, as nearly as possible, was exerted on the slat in both cases. By rearing up and looking through the top of the cage when the louder noise was made, the animal was to show its discrimination of the louder and lesser noises. It was fed at the louder noise and not fed at the lesser. The noise apparatus was manipulated at the closed side of the cage, so it was not possible the reactions were to stimuli other than the sounds. The noises were made in an irregular order.

Pet.—On the first day of the experiment, in twenty trials, the animal reacted to the food-sound, the louder noise, eight times, to the lesser noise four times and with three doubtful responses.

In the third trial (the first correct response), in the eighth and in the fifteenth, though giving the correct response to the stimulus, the cat's reactions were slow, as if in some doubt what to do. On the second day, in twenty trials, or forty trials in all, Pet reacted to the louder noise twenty times and to the lesser noise none. In the second and fourth trials it *started* to respond to the lesser noise *but stopped.* On the next day, being tested in fifteen trials, the animal made no mistakes.

We may regard the results of these experiments as positive. In the experiments on pitch discrimination, the criticism may be offered that the experimenter should have sounded the notes out of the animal's sight. This is true, but as I had no assistant, it was not practicable. However, I was careful not to give the cats any cue to the correct response, by any difference of attitude when the food notes were sounded and when the other notes were played. So it does not seem possible to attribute the reactions of the animals to anything else than the association of a certain note with food-getting, and the consequent discrimination of that note from the other notes. Moreover, several observed incidents in the course of the experiments, such as getting up at the wrong note and *getting down at once*, strengthen this conclusion. Furthermore, the looks and actions of the animals, to an unbiassed observer, would indicate such clear discrimination of the notes. We conclude, therefore, that cats, or at least some cats, discriminate musical pitch, and also discriminate noises of different degrees of intensity.

It will be noted that in the experiment in which two individuals were tested, i.e., in the discrimination of a difference of two octaves of pitch on a harmonica, while the younger animal formed the association in 45 trials, the older animal required 90 trials to perfect the association. Again, as compared with the ability of raccoons, in similar tests, of the discrimination of the difference of two octaves of pitch on a harmonica, while the cats took respectively 45 and 90 trials, the two raccoons tested required 100 and 150 trials respectively to form the association. In exactly similar experiments which the writer made on two Rhesus monkeys, one individual formed the association in 30 trials, and the other in 40. Though, from the fewness of the individuals used in these different experiments, we are not warranted in drawing final conclusions as to the comparative rapidity of the formation of such associations in cats, raccoons and monkeys, the indications, however, point to the conclusion that Rhesus monkeys form such associations with somewhat more rapidity than cats, and with considerable more facility than do raccoons under similar experimental conditions.

NOTES

A NOTE ON THE SUPPOSED OLFACTORY HUNTING-RESPONSES OF THE DOG

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Our present inability to measure or control olfactory stimuli may have some bearing on the fact that the dog's sense of smell has been avoided by careful experimental investigators. A number of problems in this field are highly interesting even though they do not lend themselves to treatment by quantitative methods. The supposed olfactory responses made by the dog in hunting are especially puzzling. At present the only available data are purely anecdotal, and these are meager, conflicting and untrustworthy.

Various assertions have been made as to the ability of the trained hunting-dog to trail his quarry. The belief is widespread that the bloodhound can follow a trail over 24 hours old without back-tracking. Let us accept provisionally a seemingly conservative statement; that a fox-hound can follow a three-hour-old trail of a rabbit without back-tracking, and assume that this is very near the limit of the dog's ability. A casual examination suffices to show the difficulty of explaining the dog's behavior.

Many hunters have said in effect that the dog follows the trail in the direction taken by the rabbit because the tracks made recently excite more intense smell-processes than do the older tracks. This explanation is not satisfactory. Suppose that in each of a series of tracks, *a*, *b*, *c*, etc., a like quantity of the same single smell-substance had been deposited by the rabbit; that the tracks had been made one second apart, and that *a* was made three hours ago. It is evident (*changes of chemical composition being excluded*) that the smell-substance is greatest in quantity when first deposited. It becomes dissipated in time so that in this case there is barely enough left in the track *a* to affect the dog.

If the smell-substance is deposited in a gaseous state, its diffusion could be represented by one of the well-known "curves of decay." The absolute intensity of the stimulus (i.e., the amount of odorous substance present in the track at a given moment of time) may, within limits, be formulized:

$$\text{Log } S_t = \text{Log } S_o - kt,$$

wherein S_o equals the amount of the substance first deposited, t the time which had elapsed since the deposit was made, and k a constant function dependent on conditions of temperature, pressure, etc.

In the case under consideration the stimulus-intensity at the track *a* is nearly zero when it is presented to the dog. The absolute difference of stimulus-intensity at *a*, *b* and *c* would have to be extremely small, since the difference in the respective values of t is of the order of one part in nearly 11,000. Further: even this difference between *a* and *b* would exist only if they were simultaneously presented. Since the dog is supposed to be following the trail of the rabbit, for him to be affected by even a part of the difference between *a* and *b* it is necessary that he travel faster than did the rabbit in making the tracks. If the dog travels at the same rate as did the rabbit, when he reaches *b* its intensity will be just equal to that of *a* when *a* was passed. Moreover, in actual practice other difficulties arise. Suppose the rabbit has run from moist ground to dry ground. The smell-substances are diffused more rapidly under conditions of relatively small humidity that under conditions of greater humidity. The stimulus-intensity of the recently made tracks on dry ground could thus be less than those made earlier on the wet ground. In such case our assumption fails to explain the dog's failure to show confusion.

But the dissipation of the smell-substance may be a complex process. For instance, it may be deposited, not in a gaseous state, but as a liquid or solid. In such case vaporization must precede diffusion. Vaporization, conditions being constant, proceeds at nearly a uniform rate in the open air. The amount of substance present in a gaseous state might thus be as great at a very advanced stage of dissipation as at an earlier stage. Since the substance to be odorous must be gaseous, we are not warranted in assuming that the stimulus-intensity is greater at a recently made track than at one made earlier, unless we know that all the smell-substance in the later track has been vaporized.

There may be other factors such as chemical changes by which the deposited substance becomes odorous, etc., but consideration of them only increases the presumption against the intensity-difference theory.

It has been suggested also that the dog may have an acute olfactory sensitivity to the *form* of the tracks made by his quarry and follow the trail from heel to toe. Certain features of the dog's behavior certainly indicate that he is *very* sensitive to differences of spatial position of olfactory stimuli. Another suggestion is that the smell-substances deposited by the different parts of the foot or body may differ specifically in stimulating quality, and that the dog is affected by this difference. Assuming either of these suggestions as a complete explanation of the dog's hunting behavior would require us to expect a bloodhound striking a man's trail at right angles, to back-track if the man had walked backward instead of forward across the field.

Dr. P. W. Cobb has suggested a simple hypothesis; that the dog's sense of direction may be due to the trailing of *ground* smell-substances. For instance: the smell-substances affecting a dog trailing a man who had crossed a mint-bed might be (1) ground + man; (2) ground + man + mint, the mint being intense; (3) ground + man + mint, the mint-smell-substances diminishing rapidly in the direction the man had taken. The hypothesis impresses the writer as being valuable, although it does not afford a complete explanation of the facts as variously alleged.

The value of careful field-tests should be apparent. The question may well be raised whether the hunting-behavior of the dog is really an olfactory response. A comparison of the field-behavior of anosmic dogs and normal dogs of the same litter and of a hunting breed, such as the beagle-hound, should prove highly interesting. It would be well worth while to ascertain as a beginning what responses a good hunting dog actually makes when introduced to trails the time and direction of which had previously been ascertained. The effect of numerous disturbing factors which could be introduced, some of which have been suggested above, ought to be quite interesting. It is to be hoped that some one with proper facilities and ample training may become interested enough to make an experimental investigation in this field.